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VOLUME 18, No. 2 NOVEMBER 1949

THE COLONIZATION OF BOMB-CRATER PONDS AT MARLOW, BUCKINGHAMSHIRE

BY TOM WARWICK
Royal (Dick) Veterinary College, Edinburgh

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1. INTRODUCTION

ERRATA

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p. 195

For 17 Helmid larvae taken at CB on 24. vi. 47 *read* 7

p. 198

For pupa *read* pupae *after Glossosoma* in Table 2.

p. 203

Insert heading 'Plant tissue and detritus (moss and phanerogam)' *between* 'Pulverized masses' *and* 'Protozoa'.

2. THE PONDS, THEIR FLORA AND FAUNA

Most of the bombs fell in a field about 1 mile south of the centre of Marlow. This field is 600 × 275 yd., and the bomb craters form a zone lying roughly north-south and measuring about 440 × 125 yd. The field is on the north bank of the River Thames opposite Bisham Abbey and is marked on the 6 in. O.S. map as being 'liable to floods'. Its top soil consists of 6–9 in. of dark brown recent alluvium containing land shells typical of marshy meadow conditions (Warwick, 1948). Underlying this is stiff alluvial clay, and this in turn covers gravel and the base of the upper chalk.

The ponds formed in some of the bomb craters [illegible] in depth and had marshy and aquatic vegetation round their margins. The deeper water in such ponds was generally somewhat turbid owing to the clayey bottom; the largest was about 8 yd. in diameter. These larger crater ponds may be expected to persist for several years. The following marsh plants fringed the deeper ponds and grew in and around the shallower ones and were found in 21 ponds in all: *Sparganium erectum, Mentha aquatica, Scirpus lacustris, Alisma plantago-aquatica, Caltha palustris, Juncus articulatus, Juncus communis, Equisetum fluviatile, Typha latifolia, Bidens cernua.*

The most frequently occurring aquatic plant was *Lemna minor*, and the following plants also occurred: *Callitriche palustris, Myriophyllum* sp., *Elodea canadensis, Hottonia palustris, Chara* sp., *Fontinalis antipyretica.*

3. THE DISTRIBUTION OF THE FAUNA

The distribution of the various species of animals collected in the ponds is shown in Table 1. Many species of aquatic insects and their larvae were also found, but as their adults can easily travel they are not dealt with here. *Potamopyrgus* (*Hydrobia*) *jenkinsi*, keeled and smooth forms, was common in the single pond in which it occurred. This particular pond was deep, and molluscs in general when present in such ponds were limited to the margin or to shallow pools amongst marsh vegetation at the edge. It was noticed, however, that this snail extended farther into the depths of the pond than was usual. Large specimens of *Limnaea palustris* were found in one pond, indicating that conditions were suitable to it. *Planorbis spirorbis* occurred in 30 ponds, and in 8 of these ponds it was noticeably common. Its variety *leucostoma* Millet was present in one pond, and in another many deformed specimens were seen in

Table 1. *Distribution of the species collected in the crater ponds*

Pond	*Potamopyrgus jenkinsi* (Smith)	*Limnaea palustris* (Müller)	*Limnaea stagnalis* (L.)	*Limnaea peregra* (Müller)	*Planorbis planorbis* (L.)	*Planorbis carinatus* (Müller)	*Planorbis vortex* (L.)	*Planorbis spirorbis* (L.)	*Planorbis albus* (Müller)	*Planorbis contortus* (L.)	*Pisidium personatum* Malm	*Asellus aquaticus* (L.)	*Gammarus pulex* (L.)	*Gasterosteus aculeatus* (L.)	*Triturus v. vulgaris* (L.)
1	.	.	.	.	.	.	.	.	.	×	.	×	.	.	.
2	.	×	.	.	.	.	×	×	.	×	.	×	.	.	.
3	.	×	.	.	.	.	.	.	.	.	.	.	.	×	.
4	.	.	.	×	.	.	.	×	.	.	.	.	×	.	.
5	.	.	.	.	.	.	.	×	.	×	×	.	.	.	.
6	.	.	.	.	.	.	.	×	.	.	.	×	×	×	.
7	.	×	.	.	.	.	.	×	.	.	.	×	×	.	.
8	.	.	.	.	.	.	.	×	.	.	.	×	.	.	.
9	.	.	.	.	.	.	×	×	.	.	.	×	.	.	.
10	.	.	.	.	.	.	.	×	.	.	.	×	×	×	.
11	.	.	.	.	.	.	.	×	.	.	.	×	×	.	.
12	.	.	.	.	.	.	.	×	.	.	.	×	×	.	.
13	.	.	.	.	.	.	.	×	.	.	×	.	.	.	.
14	.	.	.	.	.	.	.	×	.	.	.	×	.	×	.
15	.	.	.	.	.	.	.	.	×	.	.	×	×	×	.
16	.	.	.	.	.	.	.	×	.	.	.	×	.	.	.
17	.	.	.	.	.	.	.	×	.	.	.	×	×	.	×
18	.	.	.	.	.	.	.	×	.	.	.	×	.	.	.
19	.	.	.	.	.	.	.	×	.	.	.	×	.	.	×
20	.	.	.	.	.	.	.	×	.	.	.	×	.	×	×
21	.	.	.	.	.	.	.	×	.	.	.	×	.	.	.
22	.	.	.	.	.	.	.	×	.	.	.	×	.	.	×
23	.	.	.	.	.	.	.	.	.	×	.	×	×	.	×
24	.	.	.	.	.	.	.	×	.	.	.	×	.	×	×
25	.	.	.	.	.	.	.	×	.	.	×	×	.	.	.
26	.	.	.	.	.	.	.	.	.	.	.	×	.	×	.
27	.	.	.	.	.	×	.	×	.	.	.	×	.	.	.
28	.	.	.	.	.	.	.	×	.	.	×	×	×	.	.
29	.	.	×	.	.	×	.	×	.	.	.	×	.	×	.
30	.	.	.	.	.	.	.	×	.	.	.	×	×	.	.
31	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.
32	.	.	.	.	.	.	.	×	.	.	.	×	×	.	.
33	.	.	.	.	.	.	.	×	.	.	.	×	.	.	.
34	×	.	.	.	.	.	.	.	.	.	.	×	×	.	×
35	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.
36	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.
37	.	.	.	.	×	.	×	.	.	×	.	.	.	.	.
38	.	.	.	.	.	.	.	×	.	.	×	×	.	.	.
39	.	.	.	.	.	.	.	.	.	.	.	×	×	.	.
40	.	.	.	.	.	.	.	×	.	.	.	×	×	.	.
41	.	.	.	.	.	.	.	.	.	.	.	×	.	.	.
42	.	.	.	.	.	.	.	×	.	.	.	×	×	.	.
43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×

which the whorls were not all in one plane. Other species of snails which seemed to be thriving in the ponds where they occurred were *Planorbis contortus* and *Planorbis planorbis*. On the other hand, the degree of abundance when present of *Limnaea stagnalis*, *Planorbis carinatus* and *P. vortex* indicate that they will be only temporary inhabitants of these ponds. According to Boycott (1936) *Limnaea stagnalis* is more suited to 'spacious habitats', whilst *Planorbis carinatus* is usually a lake and river form and *P. vortex* prefers running water. The single occurrences of such ubiquitous snails as *Limnaea pereger* and *Planorbis albus* is doubtless due to the vagaries of dispersal.

The ponds in which *Pisidium personatum* occurred were mere puddles or overgrown. *Gammarus pulex* was associated with *Asellus aquaticus* in 15 of the 16 ponds in which it occurred. It sometimes was found in abundance in very small bodies of water amongst dense weeds. Such habitats sometimes yielded sticklebacks, *Gasterosteus aculeatus*. One specimen of the latter was infested by *Argulus foliaceus* (L.). Roach, *Rutilus rutilus* (L.), and gudgeon, *Gobio gobio* (L.), occurred abundantly in one of the larger ponds; some specimens of the former species measured 15 cm. in length. Bleak, *Alburnus alburnus* (L.), was found in another large pond. The smooth newt, *Triturus v. vulgaris*, is the only species listed in Table 1 which can of its own volition move from pond to pond.

4. DISCUSSION

(*a*) *Origin of the fauna*

The River Thames forms one boundary of the field, and the field was flooded twice between the formation of the ponds and 1945. In the second of these occasions, in February 1944, the field was completely submerged except for its extreme northern corner, which is a few feet higher than the rest. What is roughly the northern side of the field is partly bounded by a small ditch, and parallel to this is an artificial backwater leading to a boathouse. A clear stream forms the opposite boundary of the field, and into it at the south-west corner opens a stagnant ditch which commences blindly near the southern end of the cratered zone. This ditch and stream must in flood time have contributed largely to the colonizing of the ponds because of the direction of the current of the Thames. The Thames itself is obviously an important potential source. The faunas of these waters were examined, and those of ditches, streams and ponds in the Thames valley between Bourne End and Henley-on-Thames, a distance of 10½ miles by river. The number of closed ponds in the district is quite small and some are dry in the summer. In Table 2 the occurrence of gastropods, *Asellus* and *Gammarus*, in these habitats is compared with the species of animals collected in the crater ponds.

(*b*) *Factors involved in dispersal*

The main factor concerned in the colonization of these ponds will have been the flooding of the field from the River Thames. Floods could normally affect all the ponds except number 43, Table 1, and this pond is at the extreme northern corner of the field, which is a few feet higher than the rest. Perhaps significantly this pond had only *Triturus* and no aquatic plants except *Lemna minor*, which covered the surface completely.

That flooding is, in fact, actually important in the transfer of, at any rate, the active vertebrates and invertebrates is shown by the distribution of *Gasterosteus aculeatus*, *Gammarus pulex* and *Asellus aquaticus*; these species, especially the last one, have a wide distribution. Flooding would account for the occurrence of *Gasterosteus* and *Gammarus* in ponds which are little more than puddles; such loci would normally be considered most unsuitable habitats for these two species. The ditches and the backwater which bound the field could, apart from the Thames, have supplied all the species of snails found in the ponds except *Planorbis spirorbis* and *Potamopyrgus jenkinsi*. The latter is found in the Thames; *Planorbis spirorbis*, if not present in the Thames (it was not found there in the present investigation), must have arrived in some other way. Once arrived it has enjoyed some efficient method of dispersal which has enabled it to colonize many of the ponds. A possible effect of flooding on the dispersal of snails is also seen in the following striking facts. Ponds 2, 4, 5, 7, 9, 35 and 37 (Table 1), which are all fairly close together in the northern corner of the field, are the only ponds except one to have two or more species of snail. This part of the field is noticeably more lowlying and marshy than the rest. Flood water will therefore lie for a longer time, and this presumably gives a better chance for some members of the fauna to colonize the ponds submerged. Molluscan activity is at a minimum at times when flooding usually takes place. This time factor, apparently necessary for these animals to establish themselves, does not seem to be so necessary for more active types such as fish and Crustacea. Dispersal may have been helped by aquatic birds (moorhen (*Gallinula chloropus*), mallard (*Anas platyrhyncha*), heron (*Ardea cinerea*) and snipe (*Capella gallinago*) were seen), by cattle or by people fishing and by the fact that the ponds are close together.

(*c*) *Suitability of the environment for molluscs*

There is little doubt that all the crater ponds dealt with in this paper should be considered as relatively unfavourable habitats for most species of snails. They are absent in seven ponds, 28 ponds contain 1 species, five ponds 2 species, two ponds 3 species, and one pond 4 species. The average number of species of

snail per pond is 1·1. Boycott (1919) gives 2·3 as a corresponding figure for closed ponds at Aldenham; probably most of these Marlow ponds are much smaller than those dealt with by Boycott. Small size is, in itself, a factor tending to render the ponds unsuitable for many species of snails. The ponds fall into two broad classes, those which are shallow and tend to dry out in the summer, and the ponds which fill large craters and shelve deeply. Drying ponds are notoriously poor habitats, and, on the other hand, in the larger crater ponds the habitable zone for molluscs is marginal only, and even some of these ponds are without snails. Moreover, in these larger ponds the deeper water is permanently somewhat turbid from the alluvial clay. It is not surprising, therefore, to find that the commonest snail is *Planorbis spirorbis*. This species is one of the few snails which Boycott (1936) definitely associates with 'poor'

Table 2. *The occurrence of species of snails, and* Asellus *and* Gammarus, *in the aquatic habitats bounding the cratered field and near it compared with those species occurring in the crater ponds*

	Theodoxus fluviatilis (L.)	*Potamopyrgus jenkinsi* (Smith)	*Bythinia tentaculata* (L.)	*Bythinia leachii* (Sheppard)	*Viviparus viviparus* (L.)	*Valvata piscinalis* (Müller)	*Ancylastrum fluviatile* (Müller)	*Physa fontinalis* (L.)	*Limnaea palustris* (Müller)	*Limnaea stagnalis* (L.)	*Limnaea peregra* (Müller)
R. Thames at Bisham Abbey and backwater at Stoney Ware	×	×	×	×	×	.	×	×	.	×	.
Artificial backwater bounding cratered field	×	.	×	.	×	.	×	×	.	×	.
Ditch parallel to artificial backwater	.	.	.	.	.	×	.	×	.	.	.
Stream forming southern boundary	.	.	×	.	.	.	.	.	.	×	×
Stagnant ditch in south-west of cratered field	.	.	×	.	.	.	.	×	×	×	×
Stagnant ditch at Marlow	.	.	.	.	.	.	.	.	×	.	×
Gravel pit at Marlow	.	.	.	.	.	.	.	.	.	.	×
Wide running ditch, Marlow	.	.	.	.	.	×	.	.	.	.	×
Stream at Bisham	.	×	.	.	.	.	.	.	.	×	.
Small closed pond, Aston	.	.	.	.	.	.	.	.	.	×	.
Crater ponds	.	×	.	.	.	.	.	.	×	×	×

	Planorbis corneus (L.)	*Planorbis planorbis* (L.)	*Planorbis carinatus* (Müller)	*Planorbis vortex* (L.)	*Planorbis spirorbis* (L.)	*Planorbis albus* (Müller)	*Planorbis contortus* (L.)	*Planorbis crista* (L.)	*Planorbis complanatus* (L.)	*Asellus aquaticus* (L.)	*Gammarus pulex* (L.)
R. Thames at Bisham Abbey and backwater at Stoney Ware	.	×	.	×	.	×	×	.	.	×	×
Artificial backwater bounding cratered field	.	.	.	×	.	×	×	.	.	×	×
Ditch parallel to artificial backwater	.	.	.	×	.	.	.	×	×	×	×
Stream forming southern boundary	×	×	.	×	.	.	.	.	.	.	×
Stagnant ditch in south-west of cratered field	.	×	×	×	.	.	.	.	.	×	×
Stagnant ditch at Marlow	×	×	.	×	.	.	×	×	×	.	.
Gravel pit at Marlow	.	.	.	.	.	×	.	.	.	.	.
Wide running ditch, Marlow	.	.	.	×	.	.	.	.	.	.	.
Stream at Bisham	.	.	.	.	.	.	.	.	.	.	.
Small closed pond, Aston	×	.	.	.	×	×	×	.	.	×	×
Crater ponds	.	×	×	×	×	×	×	.	.	×	×

habitats. It occurs alone in 23 of the 28 ponds which only contain one species. The absence of lamellibranchs except for *Pisidium* is noteworthy. It is significant that *P. personatum* is the only species of that genus present, for it frequents the poorest type of molluscan environment. This mollusc may well have lived in marshy spots in the field before the ponds were formed.

Although there are several species of gill-breathing snails found in the locality, only one, *Potamopyrgus jenkinsi*, is found in the ponds. Even this snail, despite its hardiness and parthenogenetic habit, is found only in one pond and then not in its usual profusion. Possibly because of its method of respiration it has not often been reported from small closed ponds; but it occasionally thrives in such loci as at Mill Hill, London, and in the Manchester area. This limiting factor may have prevented *Bythinia tentaculata* from colonizing the ponds. It is found in the nearby ditches and almost certainly must have reached the ponds in one way or another; but it has not survived.

5. SUMMARY

In 44 bomb-crater ponds in a Thames-side meadow liable to floods, there were, 5 years after formation, 10 species of gastropods, 9 of which were pulmonates. Lamellibranchs were represented only by *Pisidium personatum*. *Asellus aquaticus* was widespread in distribution, and so to a lesser extent were *Gammarus pulex* and *Gasterosteus aculeatus*. A survey of neighbouring waters indicates that they have largely contributed to the fauna by flooding. The ponds are unsuitable habitats for most species of molluscs; this fact has outweighed the excellent chances of colonization by flooding from the nearby rich molluscan fauna. The characteristic and most widely distributed snail is *Planorbis spirorbis*, the only species of snail which has apparently reached the area other than by floods. Crustaceans and fish have, on the whole, colonized the ponds more successfully than the snails, partly owing to their greater activity. Snails are best represented in number of species at that corner of the field which remained flooded the longest.

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A FURTHER ECOLOGICAL STUDY OF CALCAREOUS STREAMS IN THE 'BLACK MOUNTAIN' DISTRICT OF SOUTH WALES

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(With Plates 4–6 and 2 figures in the text)

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1. INTRODUCTION

In a paper recently published in this *Journal* the writer (1948) has described the summer fauna of four torrential streams in the 'Black Mountain' district of south Wales. Of these four streams one has moderately calcareous water and a rich fauna including about 130 species; this is the river Clydach, which flows on the northern slopes. The three streams flowing on the southern slopes have very soft water which is rendered acid to varying degrees by drainage from peaty soils, and all have a much poorer fauna, including few species other than insects. This first paper dealt with variations in current speed, in the hydrogen-ion concentration and mineral salt content of the stream water and the relation between temperature and air temperature.

The present paper describes the summer fauna of the river Sawdde,* the main stream on the northern slopes of the Black Mountain, and of which the Clydach is a tributary. It includes, also, a qualitative study of the microflora of the Sawdde and the Clydach and some observations on the feeding habits of the dominant insects in this stream system, based upon the examination of the gut contents of about 600 specimens.

2. THE RIVER SAWDDE: TOPOGRAPHY, CHEMICAL NATURE, FAUNA

The river Sawdde is one of the finest trout streams in the district and is protected by the Towy Fishery Board. It has its source at an altitude of about 1700 ft. in Llyn-y-Fan-fach, a small lake lying beneath the western end of a long escarpment which 1½ miles to the east rises to about 2500 ft. About 2 miles to the north-east is the source of the river Usk. For about a mile after leaving the lake the stream flows northwards and then turns west; at station A (Fig. 1) the river is about 25 ft. wide, its bed is composed of large stones and boulders with very little gravel or sand; the stream-bed gradient and current speed vary somewhat from place to place, but there are no pools. The stream is shaded by trees and bordered by narrow strips of cultivated land.

At B, the next collecting station, the river has widened to 35 ft. and its bed has become much more uniform in gradient, so that the water flows very steadily and is up to about a foot in depth at normal level. Here and there, near the banks, there are deposits of very coarse, red gravel. Most of the stones are 6–9 in. in diameter, some are grey and some are red, and in spring, when many of the stones are bright with green algal growth, the river has a striking appearance. The right bank is shaded by trees. About 2 miles farther on the Sawdde is joined by the Clydach, and now it enters upon a kind of gorge section about 3 miles in length; here the river has cut its bed down to a level 12–15 ft. below the valley floor, and at many points flows as a narrow, deep torrent between precipitous rocky banks. The valley itself is narrow and well wooded. In this section the river is so inaccessible that no attempt was made to study the fauna, but at one point (C) some riffles are accessible where there is a thick growth of submerged moss, and here some microflora samples were taken, as described in the next section.

* Approximate pronunciation Sou'they; *sou* as in 'south'.

Photo 1. The river Clydach near station F (Pont Clydach).
The pools in the foreground are about 12 feet wide.

Photo 2. The river Sawdde at station B (Aberllechach).

Photo 3. The river Sawdde near station C (Pont-ar-llechau).
In the foreground the river is about 4 feet deep.

About 2 miles below station C the valley has widened and the river has left its 'gorge' section to flow 3–4 ft. below the level of the land, between banks of sandy soil. It is now 50–80 ft. in width and generally very shallow and swift flowing. At some points the water surface is broken from bank to bank, at others the water near the bank is almost motionless, and the stony bed is smothered with heavy deposits of silt. There is no tree shade at this station, in contrast to the other sampling stations above. About a mile below station D the Sawdde joins the river Towy, which opens to the sea near Carmarthen.

The Sawdde has an abundant flow of water which is not greatly diminished by long spells of dry weather, and very heavy rainfall is necessary to produce any substantial degree of flooding. The water is normally very clear, with no trace of peat colour, and completely free from any type of pollution. In Table 1 the result of some determinations of its main constituents are set out (for the methods employed see Jones, 1948, p. 54). The results show that the river water is moderately calcareous and has very much the same composition at all three stations. Many colorimetric pH determinations were made from time to time between April and November 1948; the results of a series made on 27 July 1948 are inserted in Fig. 1, and these show that the whole stream system is one of moderately alkaline water. On this occasion the water-level was about normal. When the river is swollen by rains its water becomes less alkaline; under conditions of slight flood the pH readings at stations A, B, C and D may change to 7·2, 7·4, 7·4 and 7·4, and a moderately heavy flood results in the pH at B, C and D dropping to 7·2. Similar changes occur in the tributary streams; chemical data for the Clydach are given in the earlier study (Jones, 1948, pp. 54–5). The oxygen determinations show that the river water is well oxygenated. These samples were taken on the afternoon of a dull November day and appear to indicate a high level of photosynthetic activity; the figure of 101·9% saturation at station D equals the highest values recorded by the writer for the river Rheidol at Aberystwyth on bright, spring days (Jones, 1949, p. 77).

The bed of the river appears to be remarkably stable. On 12 September 1948 a week of wet weather culminated in many hours of torrential rain, when all the streams in the Black Mountain district became flooded to a most abnormal degree. In the Pedol, the Garw and the Amman (the acid streams of the southern side) the force and velocity of the current was such that the stones on the stream bed were moved about, producing a groaning sound which could be heard some distance away. An examination after the flood had subsided showed that all bryophyte growth had been dislodged and swept away; the fauna had suffered so severely that hardly an insect could be found. In the case of the Sawdde little disturbance of the stream-bed was evident, most of the moss remained, and the fauna appeared to have suffered comparatively little.

At stations A, B and D a qualitative survey of the fauna was made in the summer of 1948; the dates set out at the head of Table 2, in which the animals are listed, each represent about 2 hr. collecting. The methods of collecting employed and the literature used for identification are given in earlier papers (Jones, 1941, 1948, 1949). Insects are named according to the check list of Kloet & Hincks (1945). In frequency of occurrence the various species are roughly classified into four categories: v signifies that a single specimen was taken at the collecting station; r denotes species taken in small numbers; total number up to 10; C those more common, totalling up to 100 specimens; and A the dominant animals, of which 100–200 specimens could be collected in one sample.

Table 1. *Chemical data for the river Sawdde, 27 November* 1948

River level about normal for the season. Sky overcast throughout the day. Samples for oxygen content taken at 14.00–14.30 hr. G.M.T.

Station ...	B	C	D
Water temperature (° C.)	8·0	8·3	8·3
Oxygen (mg./l.)	12·10	11·83	12·08
Oxygen (% saturation)	101·3	99·8	101·9
pH (colorimetric)	7·4	7·6	7·6
Alkali reserve (normality)	0·00108	0·00112	0·00112
Calcium (mg./l.)	21·2	22·0	21·0
Cl′ (mg./l.)	8·5	7·2	8·0
Magnesium (mg./l.)	3·5	3·5	4·0
Fe'''	Not detected		
SO_4''	Less than 1 mg./l.		

The fauna list includes about 75 species, a much smaller number than that recorded for the Clydach (about 130). In numbers of Plecoptera, Ephemeroptera and Trichoptera the Sawdde list does not differ very much from the Clydach list, and differences are most evident when we consider the Hemiptera, Coleoptera and Diptera. The chief reason for the comparatively restricted nature of the Sawdde fauna appears to be the much more restricted range of habitat afforded by the larger stream. Whereas the Clydach is very variable in gradient and has numerous pools of various sizes, the Sawdde is very uniform in gradient and has very few pools. This probably accounts for the absence of the Gerridae, Corixidae and Odonata found in the Clydach, and the occurrence in the Sawdde of only four species of Dytiscidae and one hydrophilid. At all three stations where the fauna was studied the larger stream resembles the Clydach at station G, where the summer fauna includes about 70 species. The Sawdde fauna is, of

course, essentially lithophilous; the typical lithophilous fauna, though it may be very rich in number of individuals, is not usually rich in number of species.

3. THE FLORA OF THE RIVERS SAWDDE AND CLYDACH

A qualitative survey of the flora of the Sawdde and the Clydach was begun in the spring of 1948; it was the writer's intention to determine the plant species that might afford food for the animals, and as it was soon discovered that the flora varied somewhat from time to time and from place to place, numerous examinations were made at all the collecting stations during the year. The examination dates are set out at the head of Table 3, which records all the plants seen; no quantitative sampling of the microflora was attempted; on each date specified notes were made on the distribution of *Ulothrix*, *Stigeoclonium*, *Cladophora* and other algae which could be seen with the naked eye, and scrapings were taken from stones and rocks and 'squeezings' from submerged bryophytes (as described by West & Fritsch, 1927, p. 13). On each occasion an adequate portion of the stream bed

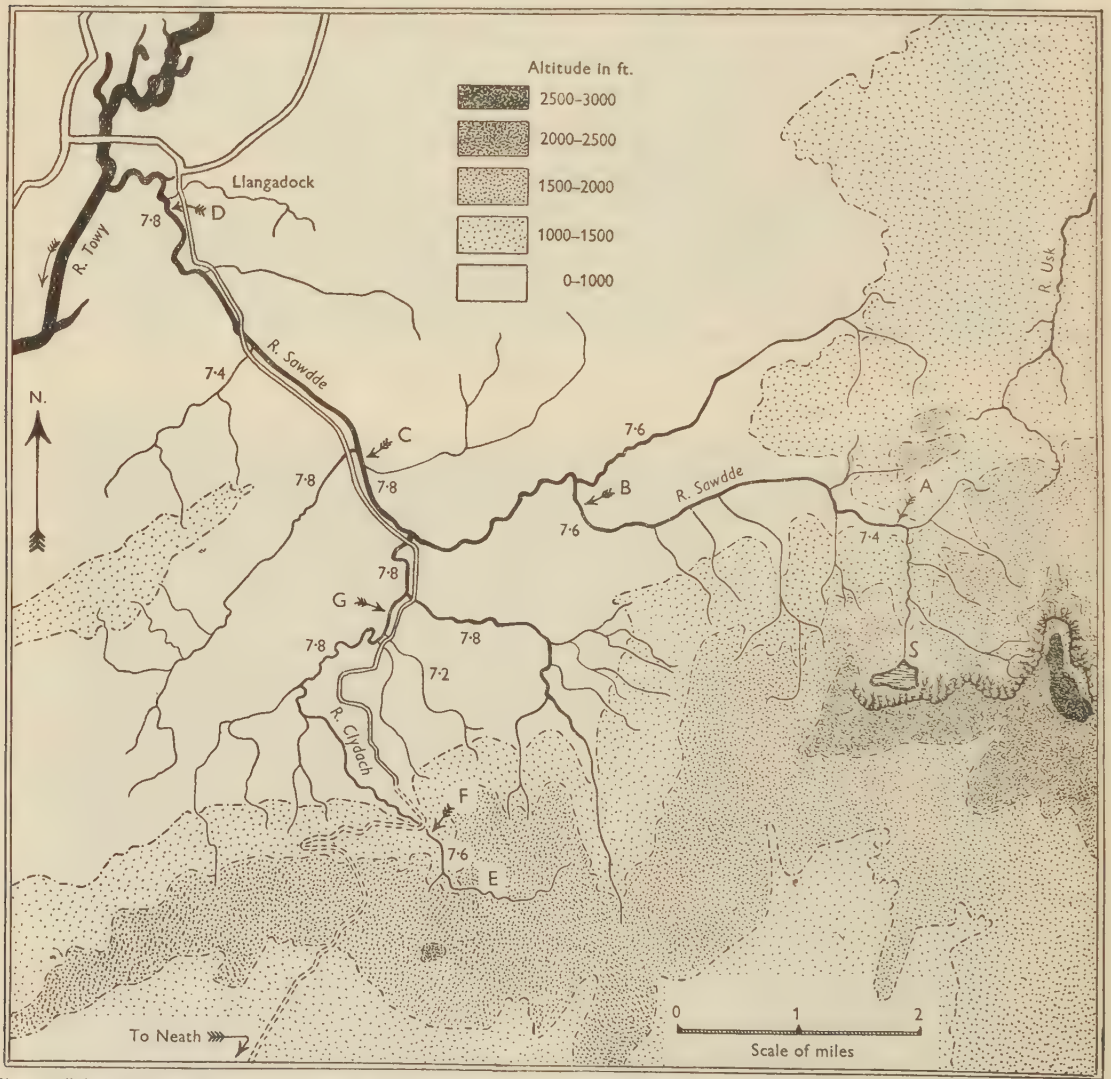

Fig. 1. Map of the river Sawdde and its tributaries. The centre of the area figured lies about 20 miles due north of Swansea Bay. Contours are drawn for 1000, 1500, 2000 and 2500 ft. A, B, C, D, E, F, G: collecting stations. *S* is the source of the river at Llyn-y-Fan-fach. The figures are a series of pH determinations made on 27 July 1948 with the river and its tributaries approximately at normal level.

Table 2. *The summer fauna of the river Sawdde*

v, very rare; r, rare; C, common; A, abundant; as explained in the text.

Habitats are given in the last column according to the following index. Where more than one figure is given the first indicates the favourite habitat and the others refer to situations where the species is less commonly found:

1. Large stones in swiftly flowing water.
2. Large stones with heavy growth of moss, in swiftly flowing water.
3. Stones and pebbles in moderately swift water.
4. Stones with dense algal growth, in moderately swift water.
5. Stones and coarse gravel in slack water near the banks.
6. Stones in still water at the river margin, with heavy deposits of silt.
7. Moss, grass and other vegetation immersed at the margins of the stream.
8. Small pools with silt-covered bottom, and heavy growth of *Cladophora*.

Collecting station ...	A	B	D	
Collecting dates (1948) ...	29 July	29 July	1 Aug.	
	27 Aug.	17 Aug.	14 Aug.	
	14 Sept.	14 Sept.	30 Aug.	
		22 Sept.	14 Sept.	Habitat
Platyhelmia				
Planaria alpina (Dana)	r	.	v	1, 3
Oligochaeta				
Nais sp.	r	.	r	5
Chaetogaster sp.	.	.	r	5
Crustacea				
Gammarus pulex (L.)	r	.	.	5
Candona sp.	.	.	r	5
Mollusca				
Ancylastrum fluviatile (Müll.)	.	C	C	3
Hydrobia jenkinsi Smith	.	.	r	8
Hydracarina				
Protzia exemia (Protz.)	r	r	.	3
Sperchon brevirostris Koen.	r	r	r	3
S. glandulosus Koen.	r	C	r	3
Diplodontus despiciens (Müll.)	.	.	r	3
Lebertia celtica Sig Thor	r	C	r	4, 5
Attractides brevirostris Halb.	C	r	A	4, 3
Hygrobates naicus (Jonst.)	r	.	r	3, 2
Megapus spinipes (C. L. Koch)	.	.	v	1
Ljania bipapillata Sig Thor	r	.	.	?
Collembola				
Podura sp.	.	r	.	7
Plecoptera				
Dinocras cephalotes (Curt.)	C	r	r	1
Perla carlukiana Klap.	C	C	A	1
Perlodes mortoni (Klap.)	v	.	.	1
Isoperla grammatica (Poda)	.	.	r	3
Leuctra fusciventris Steph.	C	C	A	3, 5
L. geniculata Steph.	.	.	A	6
Protonemura meyeri (Pict.)	C	r	.	3
Amphinemura cinerea (Oliv.)		.	r	3, 4, 5
Ephemeroptera				
Ephemera danica Müll.	.	.	r	5
Ephemerella notata Eaton	C	C	C	2, 4
Baetis rhodani (Pict.)	A	A	A	1, 2, 3, 4
Rhithrogena semicolorata (Curt.)	.	.	r	1, 3
Ecdyonurus venosus (Fab.)	C	C	r	5, 6

Table 2. (*cont.*)

Collecting station ...	A	B	D	
Collecting dates (1948) ...	29 July 27 Aug. 14 Sept.	29 July 17 Aug. 14 Sept. 22 Sept.	1 Aug. 14 Aug. 30 Aug. 14 Sept.	Habitat
HEMIPTERA				
Velia currens (Fab.)	r	C	C	5
TRICHOPTERA				
Stenophylax stellatus (Curt.) (pupae)	.	C	.	5
Sericostoma personatum (Spence)	r	C	r	5
Goera pilosa (Fab.)	r	r	.	5
Odontocerum albicorne (Scop.)	r	r	v	5
Hydropsyche instabilis (Curt.)	C	r	r	3
Plectrocnemia conspersa (Curt.)	r	r	C	6, 4
Polycentropus flavomaculatus (Pict.)	.	.	r	3
Philopotamus montanus (Donov.)	.	r	r	2
Glossosoma boltoni Curt. (pupae)	r	A	A	3
Rhyacophila obliterata McLachl.	r	C	C	1, 3
COLEOPTERA (imagines)				
Haliplus lineatocollis (Marsh.)	.	.	v	7
Oreodytes davisii (Curt.)	.	v	.	5, 3
O. septentrionalis (Gyll.)	.	r	C	6, 5, 3
O. rivalis (Gyll.)	r	r	r	5, 3
Platambus maculatus (L.)	.	.	v	8
Gyrinus natator (L.) var. substriatus Steph.	.	r	.	5
Orectochilus villosus (Müll.)	.	.	r	6
Hydraena gracilis Germ.	.	r	r	3, 2
Elmis maugei Bed.	r	v	.	3
Esolus parallelopipedus (Müll.)	C	r	r	3, 2
Limnius tuberculatus Müll.	.	r	r	2
Latelmis volkmari (Pz.)	r	r	.	3
COLEOPTERA (larvae)				
Dytiscidae	r	C	C	5
Gyrinidae	.	r	r	3
Helmidae	r	r	r	2
Helodidae	r	r	.	?
DIPTERA				
Tipula sp.	.	.	r	6
Dicranota	.	r	r	5
Limnophila sp.	.	r	r	5
Dixa sp.	C	r	r	7
Pentaneura sp.	C	C	C	3
Anatopynia sp.	.	.	r	6
Procladius sp.	.	.	v	?
Syndiamesa sp.	v	.	.	?
Cricotopus sp.	.	r	C	4
Hydrobaenus sp.	r	C	C	4
Chironomus spp.				
s.g. Endochironomus	r	r	.	4
s.g. Microtendipes	.	r	.	4
Tanytarsus sp.	.	.	r	6
Ceratopogonidae	.	v	.	5
Simulium spp. (mainly S. tuberosum Lundstr.)	C	C	r	3
Tabanus sp.	.	.	r	6
PISCES				
Phoxinus phoxinus (L.) (minnow)	.	.	C	8
Gasterosteus aculeatus L. (three-spined stickleback)	.	.	r	8
Cottus gobio L. (bullhead)	.	.	r	3
Salmo trutta L. (brown trout) S. salar L. (salmon)	Present, but not taken in the samples			

was examined, and care was taken to collect a representative sample of the microscopic forms by taking scrapings and squeezings from many points at the collecting station, including shallow and moderately deep, swift and slack water. In the laboratory the material collected in this way was mixed, and many portions of the mixture were examined at once in order to determine the more abundant algae present. Later the material was allowed to settle, and the rarer diatoms were determined by boiling the deposits with hydrochloric and nitric acids, separating the diatoms by sedimentation in the usual way, and mounting in Gurr's Clearax. At station D masses of diatoms could be collected from stones in slack water near the banks, particularly in September and October, but this could not be done at the other collecting stations where the submerged bryophytes yielded most of the algae.

In the identification of green and blue-green algae West & Fritsch (1927) and Smith (1933) were the principal works consulted; the literature used for the identification of diatoms included Boyer (1927), Van Heurck (1880–5) and Hustedt (1930). The diatom nomenclature is that of Hustedt.

No examination of plankton was made; it would appear that in shallow rivers the plankton represents 'a pale image of the benthos', from which it is almost entirely derived (Butcher, 1940, p. 210). According to their regularity of appearance in the different samples and the numbers or quantity seen, the plant species are classified as 'abundant', 'common', 'rare' or 'very rare'. A species denoted as abundant is one seen in every examination of the region specified and sometimes sufficiently abundant to be a dominant form; those denoted as common were present in moderate quantity in all or most of the samples, but were never clearly dominant types. Plants of more irregular occurrence and greater rarity are indicated as rare or very rare; diatoms classified as very rare were only seen after systematic search of the prepared slides.

This classification is, of course, very rough and covers an enormous range of abundance; thus in the case of *Gyrosigma spenceri* only two specimens were seen, while at the other extreme *Diatoma vulgare* occurred in all the samples taken at station D and usually in masses containing millions of frustules.

Of the filamentous green algae, *Ulothrix* is most widespread, and from time to time during the year was abundant at stations D and F. Growth was usually more scanty at the tree-shaded stations. At D the spring growth of this alga rendered the whole stream bed green. Two species appear to occur, one has large cells with thick walls (probably *U. zonata*), the other has small, thin-walled cells and may be *U. subtilis*. A species of *Zygnema* was seen growing abundantly at E and F on boulders and rocks over which the water pours in a thin trickle. *Stigeoclonium* appeared sporadically at C and D, but never equalled the *Ulothrix* in abundance, and its distribution was very patchy. *Spyrogyra* occurred in small, sand-bottomed pools and E and F in summer. Desmids are not common, as might be expected from the calcareous nature of the water; the only species at all common and well distributed is *Closterium leibleinii*, the commonest desmid of the Tees (Butcher *et al.* 1937, p. 118). Smith (1933, p. 565) states that rich collections of desmids are usually made only when the water has a pH of 5·0–6·0. It is probable that these plants do not flourish in swiftly flowing water even if this is somewhat acid; thus Reese (1937) found that desmids are rather rare in the river Rheidol, which has very soft water of pH 5·8–6·4. *Lemanea* was only seen at station A in spring, when it formed an abundant growth on some of the boulders. *Phormidium* occurred mainly on large, immovable stones and flat boulders in swift, shallow water. At station B patches up to 8 in. square were found. Apart from *Phormidium* the blue-green algae are comparatively rare.

The diatom flora includes about 85 species, but not many of these are common. In the Sawdde *Ceratoneis arcus* was an abundant spring species, but comparatively rare in the summer samples; this diatom was very variable in size and shape, and many curiously distorted frustules were seen. In August, *Diatoma vulgare* and *Achnanthes minutissima* appeared to be the most numerous species, and *Cocconeis placentula* was very common, except at station A. At station D the *Cocconeis* covered most of the *Cladophora*. The *Diatoma* frustules were variable in size but very constant in form, and the elongate varieties of the Tees (Butcher *et al.* 1937, pl. 8, 3*a*–3*d*) were not seen. *Achnanthes microcephala*, or at least the type form of this species, was rare except at station A.

The October samples at stations C and D contained great numbers of *Navicula viridula*, and in November this species, *Nitzschia dissipata* and *Melosira varians* seemed to have become the dominant types. Other common and well-distributed species in the Sawdde are *Synedra ulna*, *Cymbella ventricosa* and *Gomphonema olivaceum*, all three very variable in size and form. At station D the very large diatom *Didymosphenia gemminata* was abundant in August, epiphytic on the *Cladophora*.

In the Clydach the diatom samples varied from time to time and from station to station far more than those taken from the Sawdde, and tended to be characterized more by variety of species than by the dominance of particular types. *Tabellaria flocculosa* was common from time to time, and *Diatoma hiemale* var. *mesodon* was abundant in spring and autumn.

In some respects the microflora of the Sawdde-Clydach system resembles that of the upper reaches

Table 3. *The flora of the rivers Sawdde and Clydach*

v, very rare; r, rare or infrequent; C, common; A, abundant; as explained in the text.

	Sawdde				Clydach		
Station	A	B	C	D	E	F	G
Examination dates (1948) ...	10 April	10 April	24 March	24 March	10 July	24 March	24 March
	27 Aug.	29 July	1 Aug.	1 Aug.	19 Aug.	14 July	26 July
	14 Sept.	17 Aug.	22 Aug.	14 Aug.	6 Sept.	28 July	30 Aug.
	10 Nov.	14 Sept.	29 Sept.	22 Aug.	20 Sept.	22 Aug.	9 Sept.
		23 Sept.	2 Oct.	29 Sept.		16 Sept.	10 Nov.
		28 Dec.	10 Nov.	2 Oct.		2 Oct.	
				10 Nov.		10 Nov.	
				28 Dec.			
PHANEROGAMA							
Potamogeton sp.	.	.	.	.	r	.	.
BRYOPHYTA							
Aplozia riparia (Tayl.)	r	.	.	.	r	r	.
Fontinalis antipyretica L.	C	C	C	r	r	A	C
CHLOROPHYCEAE							
Ulothrix spp.	C	C	r	A	r	A	C
Microspora sp.	.	.	.	.	r	C	.
Stigeoclonium spp.	.	.	r	C	.	.	.
Cladophora sp.	r	r	r	C	.	r	r
Ankistrodesmus falcatus (Corda) Ralfs	v	v	r	r	.	.	.
Scenedesmus obliquus (Turp.) Kütz.	v	.	.	.	.	.	.
Mougeotia sp.	.	.	.	.	A	C	.
Zygnema sp.	.	.	.	.	A	A	.
Spirogyra sp.	.	.	.	.	r	r	.
Gonatozygon sp.	v	.	.	.	r	.	.
Netrium digitus (Ehr.) Itz. & Rothe	.	.	.	.	v	v	.
Roya sp.	.	.	.	.	r	.	.
Closterium spp. (mainly C. leibleinii Kütz.)	C	r	r	r	r	r	r
Tetmemorus granulatus (Bréb.) Ralfs	.	v	.	.	.	.	.
Euastrum verrucosum Ehr.	v	.	.	.	.	.	.
E. elegans Bréb.	v	.	.	.	.	.	.
E. didelta (Turp.) Ralfs	.	.	.	.	r	.	.
Cosmarium spp.	r	r	r	r	r	r	r
Micrasterias truncata (Corda) Bréb.	.	.	.	.	.	.	v
M. denticulata Bréb.	.	.	.	.	v	.	v
Staurastrum spp.	.	.	.	.	.	.	r
Xanthidium armatum (Bréb.) Rab.	.	.	.	.	.	v	.
Hyalotheca dissiliens (Sm.) Bréb.	.	.	.	.	.	.	v
RHODOPHYCEAE							
Batrachospermum moniliforme Roth.	.	.	.	.	r	.	.
Lemanea mammillosa Kütz.	r	.	.	.	.	.	.
MYXOPHYCEAE							
Merismopedia sp.	.	.	.	v	.	.	.
Synechococcus sp.	r	.	.	.	.	.	v
Chamaesiphon sp.	.	r	r	.	r	r	.
Phormidium spp.	r	C	r	r	r	C	r
Nostoc sp. (young spherical colonies)	r	.	.	v	.	.	r
Tolypothrix sp.	r	v	.	.	.	.	.
Rivulariaceae sp.	.	.	.	.	.	r	.

Table 3. (*cont.*)

	Sawdde				Clydach		
Station	A	B	C	D	E	F	G
Examination dates (1948) ...	10 April	10 April	24 March	24 March	10 July	24 March	24 March
	27 Aug.	29 July	1 Aug.	1 Aug.	19 Aug.	14 July	26 July
	14 Sept.	17 Aug.	22 Aug.	14 Aug.	6 Sept.	28 July	30 Aug.
	10 Nov.	14 Sept.	29 Sept.	22 Aug.	20 Sept.	22 Aug.	9 Sept.
		23 Sept.	2 Oct.	29 Sept.		16 Sept.	10 Nov.
		28 Dec.	10 Nov.	2 Oct.		2 Oct.	
				10 Nov.		10 Nov.	
				28 Dec.			
BACILLARIAE							
Melosira varians Ag.	.	.	r	A	.	.	.
M. arenaria Moore	r	v	.	.	.	.	.
Cyclotella sp.	r	.	.	.	.	.	.
Tabellaria flocculosa (Roth.) Kütz.	r	r	r	r	C	C	C
T. fenestrata (Lyngb.) Kütz.	v	v	.	.	.	v	v
Diatomella Balfouriana Grev.	v	v	.	.	.	.	v
Meridion circulare Ag.	r	r	r	r	r	C	C
M. circulare var. constrictum (Ralfs) Van Heurck	v	r	.	.	.	.	v
Diatoma vulgare Bory	r	C	A	A	.	r	C
D. hiemale (Lyngb.) Heib.	.	r	r	.	.	C	.
D. hiemale var. mesodon (Ehr.) Grun.	r	r	r	r	.	A	r
Fragilaria capucina Desmaz. / F. intermedia Grun	r	r	r	C	.	r	r
F. construens (Ehr.) Grun.	.	r	v	.	.	.	.
Synedra ulna (Nitzsch.) Ehr.	C	C	C	C	r	C	C
S. acus Kütz. ?	r	r	.	.	.	.	.
Ceratoneis arcus Kütz. / C. arcus var. amphioxys (Rabh.)	A	A	A	A	r	C	C
Eunotia arcus Ehr. / E. arcus var. fallax Hust.	A	r	r	r	r	C	C
E. pectinalis (Kütz.) Rabh. / E. pectinalis var. minor (Kütz.) Rabh.	A	C	r	r	C	C	r
E. lunaris (Ehr.) Grun.	r	.	.	.	.	C	.
E. robusta Ralfs var. tetraodon (Ehr.)	.	.	.	.	v	.	.
E. tridentulata Ehr.	v	.	.	.	.	.	.
Achnanthes coarctata (Bréb.) Grun.	.	v	v	v	.	.	.
A. lanceolata Bréb. / A. lanceolata var. elliptica Cleve	r	r	r	r	r	C	r
A. microcephala Kütz.	C	r	r	r	.	r	r
A. minutissima Kütz. / A. minutissima var. cryptocephala Grun. / A. linearis W. Smith	C	A	A	A	r	C	A
Rhoicosphenia curvata (Kütz.) Grun.	v	r	r	r	.	r	r
Cocconeis placentula Ehr.	r	C	C	A	r	C	A
C. pediculus Ehr.	.	.	r	C	.	.	.
Navicula rotaeana (Rabh.) Grun.	v	v	v	r	.	v	v
N. cryptocephala Kütz.	r	r	C	r	r	r	C
N. anglica Ralfs	.	v	v	r	.	r	v
N. gracilis Ehr.	v	v	C	r	.	.	.
N. rhyncocephala Kütz.	r	r	.	.	r	r	.
N. viridula Kütz.	r	A	A	A	v	r	A
N. dicephala (Ehr.) W. Smith	.	.	v	.	.	.	v
Pinnularia leptosoma Grun.	.	r	.	r	.	.	.
P. interrupta W. Smith	r	.	.	.	r	.	.
P. brebissonii (Kütz.) Cleve	v	.	v	.	.	r	.
P. major (Kütz.) Cleve	r	v	v	.	.	.	.
P. viridis (Nitzsch.) Ehr.	r	r	r	.	r	r	r
P. subcapitata Greg.	.	.	v	.	r	r	r

Table 3. (*cont.*)

	Sawdde				Clydach		
Station	A	B	C	D	E	F	G
Examination dates (1948) ...	10 April	10 April	24 March	24 March	10 July	24 March	24 March
	27 Aug.	29 July	1 Aug.	1 Aug.	19 Aug.	14 July	26 July
	14 Sept.	17 Aug.	22 Aug.	14 Aug.	6 Sept.	28 July	30 Aug.
	10 Nov.	14 Sept.	29 Sept.	22 Aug.	20 Sept.	22 Aug.	9 Sept.
		23 Sept.	2 Oct.	29 Sept.		16 Sept.	10 Nov.
		28 Dec.	10 Nov.	2 Oct.		2 Oct.	
				10 Nov.		10 Nov.	
				28 Dec.			
BACILLARIAE (*cont.*)							
P. gibba Ehr.	.	v	.	.	.	.	.
P. lata (Bréb.) W. Smith	.	v	.	.	.	.	.
Neidium iridis (Ehr.) Cleve	.	.	.	.	.	r	.
Diploneis elliptica (Kütz.) Cleve	v	v	.	.	r	v	.
Stauroneis phoenicenteron Ehr.	v	v	.	.	v	.	.
S. anceps Ehr.	.	v	v	.	.	v	.
Amphipleura pellucida Kütz.	v	r	.	.	v	r	r
Frustulia rhomboides (Ehr.) De Toni	.	v	.	.	.	v	.
F. vulgaris Thwaites	v	r	v	.	.	v	v
Gyrosigma Spenceri (Queckett) Cleve	.	v	.	.	.	.	.
Gomphonema acuminatum Ehr. (mainly var. coronatum (Ehr.) W. Smith)	r	r	r	r	C	r	r
G. constrictum Ehr.	r	.	r	.	.	.	r
G. parvulum (Kütz.) Grun.	r	r	.	r	r	C	r
G. angustatum (Kütz.) Rabh.	.	.	v	r	.	r	v
G. lanceolatum Ehr.	r	.	.	r	.	.	.
G. intricatum Kütz.	r	.	r	r	.	r	.
G. olivaceum (Lyngb.) Kütz.	r	C	C	C	.	C	C
Didymosphenia gemminata (Lyngb.) M. Schmidt	r	r	r	A	.	.	r
Cymbella cuspidata Kütz.	.	.	.	.	.	r	v
C. affinis Kütz.	v	.	v	r	.	r	.
C. sinuata Greg.	r	r	C	C	.	r	C
C. lanceolata (Ehr.) Van Heurck	v	.	v	.	.	v	v
C. cistula (Hempr.) Van Heurck	C	r	r	r	.	C	r
C. helvetica Kütz.	r	r	r	r	r	C	r
C. angustata (Kütz.) Cleve	.	.	.	.	.	.	v
C. ventricosa Kütz.	C	C	C	C	r	C	C
C. prostrata (Berk.) Cleve	.	v	v	r	.	v	.
C. delicatula Kütz.	r	v	v	.	.	C	.
Ampora ovalis Kütz.	.	v	.	v	v	.	.
Epithemia argus Kütz.	r	.	.	.	r	.	.
E. zebra (Ehr.) Kütz.	.	v	v	.	r	r	.
E. gibberula (Ehr.) Kütz.	.	.	.	.	.	r	.
Rhopalodia gibba (Ehr.) O. Müll.	r	.	.	.	.	v	.
Nitzschia linearis W. Smith	v	r	r	v	.	.	v
N. palea (Kütz.) W. Smith	.	r	r	C	.	.	r
N. dissipata (Kütz.) Grun.	.	.	r	A	.	.	.
N. sinuata (W. Smith) Grun.	v	.	v	.	.	.	.
N. acicularis W. Smith	.	.	v	v	.	.	.
Hantzschia amphioxys (Ehr.) Grun.	.	.	.	.	.	r	v
Denticula sp.	.	.	.	.	.	r	r
Cymatopleura solea (Bréb.) W. Smith	.	v	v	.	.	.	.
Surirella ovata Kütz.	v	r	r	r	.	.	.
S. robusta Ehr.	.	r	.	.	.	.	.

of the Tees, where *Diatoma vulgare, Achnanthes microcephala, Gomphonema olivaceum, Cocconeis placentula, Navicula viridula* and *Cymbella ventricosa* are common diatoms (Butcher *et al.* 1937, p. 69). *Cocconeis placentula, Achnanthes minutissima* and *Gomphonema olivaceum* are dominant diatoms in the unpolluted rivers Test and Itchen, which contain a plentiful supply of calcium and other mineral salts (Butcher, 1946, pp. 274, 283).

The only phanerogam seen in the Clydach is a species of *Potamogeton*, of which a little grows at one point in region E. No phanerogams occur in the main stream of the Sawdde. The only common bryophyte is the moss *Fontinalis antipyretica*, which is generally distributed throughout the Sawdde system, including all its main tributaries. The stability of the river bed probably accounts for the abundance of the moss, which grows most luxuriantly in the cascade section of the Clydach at region F.

It would appear from this examination of the flora of the Clydach and the Sawdde that the chief plants available as food for the fauna are *Fontinalis, Ulothrix* and a considerable variety of diatoms. Less abundant and more irregularly distributed plants are the liverwort, *Aplozia*, the green algae *Zygnaema, Microspora, Mougeotia, Cladophora* and *Stigeoclonium*, and the blue-green alga *Phormidium*. In addition to plant material actually growing in the water there is a plentiful supply of leaves from the trees and other plants on the banks, for the Sawdde valley is well wooded with coniferous and deciduous trees. The extent to which the plant food supply is utilized by some of the chief insect species is discussed in the next section.

4. THE FOOD OF THE DOMINANT INSECT SPECIES

(*a*) *Literature*

Throughout zoological literature there is scattered a great deal of information regarding the feeding habits of aquatic insects. Not all this information is accurate, some of it is largely conjecture, and it would appear that observations on the feeding habits of particular species have led to general statements recklessly applied to related species and genera, and even all insects of the same order. Thus Rousseau (1921, p. 279) and more recently Mellanby (1942, p. 128) have stated that all stonefly nymphs are carnivorous, a generalization which is far from correct.

Most investigators have confined their attention to particular genera, families or orders. Rawlinson (1939, p. 405) has dealt with the method of feeding in *Ecdyonurus*, and has reviewed earlier literature dealing with the feeding habits of mayfly nymphs; Needham, Traver & Hsu (1935, p. 224) have supplied some information regarding the nymphs of North American Ephemeroptera. Frison (1929, p. 365) has reviewed the literature on the feeding habits of Plecopteran nymphs, and Hynes (1941, p. 529) has studied all the British species of this order. Tillyard (1917, p. 329) makes some general observations on the food of the naiads of the Odonata. Lloyd (1921) and Ross (1944, p. 4) have described the food of North American trichopteran larvae; Slack (1936) has studied a number of British species, mainly of the case-carrying type, and Nielsen (1948, p. 163) describes the mode of feeding of the Hydroptilidae.

In regard to the Coleoptera it appears to be generally accepted that the Gyrinidae and Dytiscidae are carnivorous and the Hydrophilidae and Haliplidae phytophagous (Ward & Whipple, 1918, pp. 907–8; Miall, 1903, pp. 33–89), but little detailed investigation of the food and feeding habits of the water beetles appears to have been made except in the case of *Dytiscus* and a few other genera. Alexander (1920, p. 717) has discussed the feeding habits of the larvae of the Tipulidae. Smart (1944, p. 20) and Puri (1925, p. 298) deal with the food of *Simulium*, and Goeghtgebuer (1927, 1928, 1932) supplies information regarding the food of some genera of the Chironomidae.

The food of aquatic insects is determined to a considerable extent by the environment in which they live; thus *Polycentropus flavomaculatus* in Lake Windermere feeds upon small Crustacea (Moon, 1934), in the river Amman on chironomid larvae (Jones, 1948); and in the river Rheidol I have found that it feeds mainly upon *Rhithrogena* and *Baetis*; nymphs of *Nemoura vallicularia* under natural conditions will eat decaying leaves and a great variety of desmids, diatoms and other unicellular algae, but in captivity they will live entirely upon elm leaves (Wu, 1923, p. 39). Puri (1925, p. 298), reviewing the literature relating to the food of *Simulium*, remarks that larvae of different species collected from the same locality always show more or less the same type of gut contents, and that the wide divergencies in the accounts given by different investigators of the food of *Simulium* larvae can be attributed to the insects they examined having come from different localities. The very abundance of a plant may force phytophagous insects to eat it; thus Needham *et al.* (1935, p. 225) describe a stream in which the diatom *Meridion* may appear in such profusion as to cover every available object; mayfly nymphs collected have their stomachs full of this diatom and little else.

In this study the writer has attempted to gather some information on the feeding habits of the dominant insect species of the Clydach-Sawdde stream system, taking into account, as far as possible, the type of fauna present, the flora and the general nature of the environment. During July and August 1948 about 600 specimens were examined for gut

contents, and an attempt was made to identify as accurately as possible the nature of the food, whether plant or animal.

(*b*) *Methods*

In the case of large, carnivorous insects such as *Perla*, *Dinocras* and *Plectrocnemia* the specimens were dropped into 70% alcohol at the collecting station and could be examined, if necessary, 2 or 3 days later, though removal of the gut is facilitated by prompt examination, and vegetable food, if present, can be more easily recognized. The head of the insect is cut off, the end of the abdomen is cut off to free the hind-gut, the alimentary canal is pulled out and placed on a microscope slide. Using a low-power binocular the anterior portion of the gut is slit open with a cutting needle, the contents removed, spread on the slide and covered with a drop of dilute glycerine and a cover-slip for examination with the microscope. Considerable care is necessary in removing animals from the gut in order that the food of the prey is not mistaken for food eaten by the predator; here, knowledge of the food of the prey is very helpful in preventing mistakes. With trichopteran larvae an alternative method of removing the gut was found very successful; the larva, killed with 70% alcohol, is placed on its side on the microscope slide, the head is held with one pair of forceps, and with another pair the base of one front leg is gripped and pulled backwards so that the body wall is torn down the side of the thorax and abdomen. It is then a very simple matter to extract the gut. The gut contents in a large trichopteran larva may be very bulky, and five or six preparations may have to be made in order to examine it all. In the case of the smaller insects studied, particularly omnivorous and phytophagous types, it was found that the examination of specimens placed in alcohol was not very satisfactory, as the removal of the gut and its contents might be very difficult. Here the procedure adopted was to collect the specimens, transport them to the laboratory as quickly as possible, and begin the examination of the gut contents at once. The live insect is placed on the microscope slide, quickly decapitated with a cutting needle, the end of the abdomen is cut off; usually the longitudinal muscles of the body contract so that the gut protrudes from the prothorax and is readily extracted. Usually it was possible to make successful determinations of the food up to about 2 hr. after capture.

In the case of adult Dytiscidae and Gyrinidae the removal of the fore-gut is very simple; the beetle is killed with 70% alcohol, or with chloroform water, the thorax is gripped with one pair of forceps, and another is used to pull the head away from the body; the alimentary canal breaks at the anterior end of the mesenteron, and gizzard and crop come away with the head.

The part of the alimentary canal where recently eaten and recognizable food was found varied in the different species studied. In *Perla* and *Dinocras* and the Coleoptera identifiable material is generally found in the fore-gut only; in *Leuctra*, the Ephemeroptera and the Trichoptera the whole of the mid-gut may contain materials that can be recognized. The larger stoneflies swallow their prey entire, so that its identification is easy; in the case of insects which bite their prey into pieces the food organism can usually be recognized by some characteristic feature; thus ecdyonurid nymphs can be identified by their brush-bearing mouthparts even if extensively fragmented, *Simulium* larvae by their feeding brushes and anal hook circles, small Plecoptera by the form of the tarsus, and the Tanypodinae by the lingua. When many much-fragmented prey organisms of the same kind occurred in one gut, the number eaten was estimated by counting the number of heads present.

The results are summarized in Table 4. 'Gut contents digested' means that the anterior part of the gut contained a soupy mass of food in which nothing could be recognized. 'Detritus' means amorphous vegetable matter mixed with fine grit and occasionally with a few empty algal cells. The presence of algae is indicated only when the cells contained chloroplasts, showing that the insect had swallowed the living plant, odd empty cells were ignored. Diatoms are indicated as present only when the gut contained what appeared to be a significant number; a few diatoms, mainly empty frustules, were always present when the gut contained detritus.

The unbracketed numbers opposite the list of 'foods' signify the number of specimens in which this food was found. The bracketed numbers inserted in the case of some of the predatory species indicate the numbers of prey organisms found in the total number of specimens examined. Thus in the case of *Perla carlukiana* 14 of the specimens examined had *Simulium* larvae in the gut; the total number of *Simulium* larvae seen in the 75 *Perla* nymphs examined was 31.

(*c*) *Plecoptera*

Perla and *Dinocras* appear to be the dominant predatory insects, feeding on a wide range of food organisms, particularly *Baetis*, *Ephemerella*, chironomid larvae and *Simulium*. The chironomid larvae were mainly Orthocladiinae. It was found that *Baetis* and *Ephemerella* nymphs present in the gut contents could seldom be distinguished with certainty, though both genera could easily be distinguished from *Ecdyonurus* by the combs on the tarsal claws; hence the two former genera are grouped together in Table 4. One *Dinocras* nymph contained vegetable

Photo 4. The river Sawdde at Station D (Careg-Sawdde).

food only (*Fontinalis* and *Ulothrix*); one had several desmids in its crop together with insect food. None of the *Perla* nymphs appeared to have been feeding on plant food alone, but the crops of four contained green masses of *Ulothrix* as well as a variety of insect food.

Most of the insects eaten by these large stonefly nymphs appeared to have been swallowed entire. One *Perla* specimen contained 8 *Baetis* and one contained 12 chironomids and 3 *Protonemura* nymphs, but in most of the specimens the meal tended to consist of a small number of prey of moderate or large size rather than a large number of small animals. The trichopteran larvae eaten were of considerable size, one sufficing to fill the stomach of the predator. At other times of the year, of course, very small prey may form a greater proportion of the food. *Perla* appears to have a larger appetite than *Dinocras*; thus 46 *Dinocras* nymphs contained insect food totalling about 71 prey individuals, while the 40 *Perla* nymphs which contained recognizable food had eaten 191 insects.

In the streams of the Lake District *Perla carlukiana* appears to be more partial to vegetable food, for Hynes (1941, p. 530) found that 16% of the specimens he examined contained vegetable food only, and only 50% had fed exclusively on animal matter. The corresponding figures for *Dinocras* (*Perla cephalotes* in Hynes's Table) are 4 and 64%.

Leuctra fusciventris is herbivorous—detritus, leaf fragments, green algae and diatoms being its chief foods. The diatom feeders were among those captured at station D, and the chief genera of diatoms present were *Achnanthes*, *Cocconeis*, *Cymbella* and *Gomphonema*. *Leuctra geniculata* appears to feed mainly on detritus, though many specimens contained leaf fragments or green algae; the relative amount of these food substances present was very small. If detritus is the favourite food of *L. geniculata*, this would explain its occurrence at station D, where much detritus appears to be deposited in the stony shallows. Lestage (1920) has suggested that the peculiar processes on the antennae, which distinguish nymphs of this species from others of the genus, are an adaptation for burrowing.

Protonemura meyeri is common in the Sawdde at station A, but the specimens taken during the summer were too small for satisfactory examination. Hynes's data (1941, p. 530) show that it feeds mainly on 'higher plant and moss tissue'.

(*d*) *Ephemeroptera*

Of the dominant mayfly species in the stream system studied *Baetis rhodani* and *Ephemerella notata* are generally distributed. *Ecdyonurus venosus* is common at stations A, B, F and G. In the summer of 1948 *Siphlonurus lacustris* occurred only at station E in shallow pools with silt-sand bottom and fringed with grasses. Table 4 shows that these insects subsist on vegetable matter and detritus, but there are definite differences in the diets of the four species. *Ecdyonurus* is the chief detritus feeder, the gut being usually full of soft, amorphous matter mixed with much fine grit and sometimes very small fragments of moss. In some of the specimens diatoms were abundant; *Cocconeis*, *Achnanthes*, *Tabellaria*, *Ceratoneis* and *Synedra* were the main genera represented. Whether these diatoms were alive when eaten or were dead frustules forming part of the detritus was not clear. *Baetis* appeared to eat moss, detritus, green algae and diatoms in various proportions at the different stations. The main food of *Siphlonurus* appears to be detritus and leaf fragments, and *Ephemerella* seems to subsist chiefly on *Fontinalis* and *Ulothrix*. On 14 July 1948, 14 specimens of *Ephemerella* from station F were examined, and in these the moss was the main food; 6 specimens contained little else. On this date there was very little *Ulothrix* growing on the stream bed. A fortnight later an abundant growth of *Ulothrix* had appeared at this station. A further batch of *Ephemerella* was then examined, and in these the green alga was the main food present.

(*e*) *Trichoptera*

Six species of Trichoptera were studied. *Plectrocnemia* and *Rhyacophila* appear to be entirely carnivorous, the prey of the former displaying considerable variety. One *Rhyacophila* larva contained about 10 chironomid larvae, but 3–5 was usually the number of prey insects present. Ross (1944, p. 4) states that he has seen larvae of this genus with 40–60 chironomids in the gut. *Hydropsyche* appeared to be omnivorous but with a decided preference for animal food, for all those examined which had recognizable material in the gut had eaten animal food and 7 had eaten animal food only. *Hydropsyche* larvae are said to catch their prey in the net-traps; they spin amidst weeds and stones, but whether they obtain all their food in this way is not clear.

Philopotamus is mainly a diatom feeder; the gut often contained some gritty detritus and a few small fragments of moss, but in a typical case its main contents is a smooth mass of millions of diatoms in which a considerable variety of species are represented. Lloyd (1921, p. 109) states that the larvae of the Philopotamidae collect masses of diatomaceous ooze with the nets they spin. The *Hydropsyche* larvae examined had fed mainly upon small insects; only 3 specimens had any significant number of diatoms in the gut, and if it is correct that *Hydropsyche* and *Philopotamus* collect most of their food with nets some explanation is necessary for the difference in their diets. Perhaps the nets spun by the latter have a much closer mesh, and it may be that the former

Table 4. *Summary of observations on the gut contents of some of the dominant insect species*

(Explanation in the text, § 4 (*b*)).

	Plecoptera				Ephemeroptera				Trichoptera						Coleoptera	
Collecting station ...	A, F	A, B, D, G	D, F	D	B, F	D, F	D, F	E	A, B, D, G	G	D, E	F	B	B	F	D
Species ...	*Dinocras cephalotes*	*Perla carlukiana*	*Leuctra fusciventris*	*Leuctra geniculata*	*Ecdyonurus venosus*	*Baetis rhodani*	*Ephemerella notata*	*Siphlonurus lacustris*	*Rhyacophila obliterata*	*Hydropsyche instabilis*	*Plectrocnemia conspersa*	*Philopotamus montanus*	*Sericostoma personatum*	*Odontocerum albicorne*	*Oreodytes rivalis*	*Oreodytes septentrionalis*
No. of specimens examined	70	75	30	25	27	33	49	38	43	25	29	24	22	12	36	41
No. with the anterior part of the gut empty	16	25	3	1	2	1	3	—	5	1	8	6	—	—	11	16
No. with the gut contents digested	7	10	1	6	2	1	4	—	9	1	3	3	3	4	3	3
Gut contents:																
Detritus	—	—	17	16	22	25	11	38	—	—	—	9	6	6	—	—
Leaf fragments (*Fontinalis*)	1	—	15	14	6	—	21	—	—	9	—	2	—	—	1	—
Leaf fragments (various other plants)	—	—	—	—	—	—	—	35	—	—	—	—	18	2	—	—
Algae:																
Ulothrix	1	4	3	3	1	13	31	6	—	12	—	1	4	8	—	—
Microspora	—	—	—	—	—	—	—	10	—	—	—	—	—	—	—	—
Stigeoclonium	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Cladophora	—	—	—	3	—	—	1	—	—	—	—	—	4	—	—	—
Cosmarium	1	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—
Other green algae	—	—	5	7	—	6	—	—	—	12	—	1	4	8	—	—
Batrachospermum	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Phormidium	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—
Diatoms	—	—	6	—	10	7	7	6	—	3	—	15	5	1	1	—
Crustacea:																
Copepoda	—	—	—	—	—	—	—	—	—	—	1 (1)	—	—	—	—	1
Gammarus pulex	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—

PLECOPTERA (nymphs):																
Perlidae	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Chloroperla sp.	—	—	—	—	—	—	—	—	—	—	1 (2)	—	—	—	—	—
Leuctra sp.	2 (2)	1 (1)	—	—	—	—	—	—	—	1 (1)	1 (1)	—	—	—	—	—
Protonemura sp.	—	2 (4)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
EPHEMEROPTERA (nymphs):																
Baetis sp. Ephemerella sp.	20 (29)	32 (84)	1 (1)		—	—	—	—	9 (9)	16 (26)	5 (8)	—	—	4 (4)	7	6
Ecdyonurus sp.	2 (2)	—			—	—	—	—	2 (2)	—	1 (1)	—	—	—	—	—
TRICHOPTERA (larvae):																
Rhyacophila sp.	2 (2)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hydropsyche sp.	1 (1)	1 (1)	—	—	—	—	—	—	1 (1)	—	1 (1)	—	—	2 (2)	—	—
Glossosoma sp.	—	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Philopotamus sp.	5 (7)	3 (3)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
TRICHOPTERA (imago):																
Sericostoma personatum	—	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
COLEOPTERA:																
Haliplus sp. ? (imago)	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dytiscid larvae	1 (1)	—	—	—	—	—	—	—	—	—	1 (1)	—	—	—	—	—
Helodid larvae	—	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
DIPTERA (larvae):																
Pedicia sp. ?	—	—	—	—	—	—	—	—	1 (1)	—	—	—	—	—	—	—
Dicranota sp.	—	—	—	—	—	—	—	—	2 (2)	—	—	—	—	—	—	—
Simulium spp.	2 (3)	14 (31)	—	—	—	—	—	—	11 (22)	4 (5)	6 (10)	—	—	—	—	1
Anatopynia sp.	1 (1)	1 (1)	—	—	—	—	—	—	—	—	1 (1)	—	—	—	—	—
Pentaneura sp.	1 (1)	1 (1)	—	—	—	—	—	—	—	—	2 (4)	—	—	—	—	—
Cricotopus sp.	—	—	—	—	—	—	—	—	2 (6)	—	1 (1)	—	—	—	—	2
Tanytarsus sp.	—	1 (1)	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Other Chironomidae	8 (21)	17 (58)	—	—	—	—	—	—	13 (37)	13 (18)	3 (4)	—	—	—	11	14
DIPTERA (imagines):																
Species not identified	1 (1)	—	1 (1)	—	—	—	—	—	—	—	1 (1)	—	—	—	2	—
Animal remains not identified	5	3	1	—	—	—	—	—	5	6	5	—	—	3	3	4

supplements the net-caught food with prey caught in the normal way.

The chief case-carrying Trichoptera in this stream system are species with heavy cases made of gravel and small stones. Pupae of *Glossosoma boltoni* were abundant, but only 2 larvae were found, and in these the gut contained only green algae. The main food of the *Sericostoma* larvae appeared to be the dead leaves of deciduous trees, the stomach containing hundreds of small, square pieces. *Odontocerum* appears to be omnivorous, but only 12 specimens could be found. Of these 8 contained recognizable food, including animal and plant material.

(*f*) *Coleoptera*

Oreodytes rivalis and *O. septentrionalis* are the common Dytiscidae. These little beetles appear to feed mainly on mayfly nymphs and chironomid larvae, but usually only isolated pieces of the prey are found in the crop, and it is rare to find an entire insect. Frequently the crop of the beetle contained only the tail end of one chironomid, or perhaps two heads with small portions of the thorax; sometimes only the legs of a mayfly nymph would be present. The crop of *Oreodytes* is very small and about three heads of small midge larvae are sufficient to fill it. Exactly how these small Dytiscidae feed is not clear; perhaps they kill the prey and swallow portions of it, perhaps they search for and eat pieces of insects killed by other predators or by movements of the stones on the stream bed. The high proportion of specimens with empty crops suggests that they feed at irregular intervals.

Seven specimens of *Orectochilus villosus* from station D were also examined; in each case the crop was full, but its contents was so fragmented that it could not be identified with certainty. The main prey present appeared to be *Velia currens*, which was common on the surface of the water where the beetles were swimming.

(*g*) *Diptera*

The gut contents of 24 *Simulium tuberosum* larvae from stations A and F were examined, and it was found possible to identify most of the food present in the alimentary canals of many *Simulium* found in the *Perla* specimens examined, but the species of these larvae could not be determined. The gut contents was much the same in all cases—a mixture of small fragments of moss and other leaves, short lengths of *Ulothrix* and other filamentous algae, diatoms and gritty detritus; two contained some *Ankistrodesmus* and one a little of the blue-green algae *Tolypothrix* and *Merismopedia*. No cases of cannibalism were seen, as reported by Smart (1944, p. 20). No attempt was made to study the gut contents of the chironomid larvae; in this group accurate identification is so difficult, particularly in the Orthocaldiinae, that specimens can be referred with certainty only to genera including a wide range of species, and it would appear that without accurate specific identification observations on the feeding habits of these larvae would not add to present knowledge.

(*h*) *General observations*

The foregoing results show that in this particular habitat *Baetis*, *Ephemerella*, *Simulium* and chironomid larvae are the most frequent prey of the carnivorous species. This is to be expected, for they are numerous, live in the swift current inhabited by the predators, and are not equipped with any form of protection. There are other common species which are not eaten to the same extent. *Ecdyonurus venosus*, though very common at most parts of the stream system, appears to escape the predatory Plecoptera and Ephemeroptera because it lives not in the swift current of midstream but in slack water near the banks, where the detritus on which it feeds accumulates, and it would appear that the flattened body shape of this species is not so much an adaptation for living in swift currents as one for creeping among tightly packed stones. *Glossosoma boltonii*, one of the most abundant insects in the Sawdde, is probably saved from being eaten by its massive, stony house. *Ancylastrum* is well protected by its smooth, conical shell. *Gammarus pulex* is plentiful in the upper part of the Clydach but is not preyed upon by any of the species studied; two *Oreodytes* had small pieces of *Gammarus* in their crops, but these contained no muscle and appeared to be moults. It may be that the large stoneflies, which like to swallow their prey entire, find the bristly Crustacean difficult to eat. The fishes are the chief enemies of *Gammarus pulex*; all the species recently studied by Hartley (1948) appeared to feed on it. The Hydracarina are another notable missing group in the list of food organisms in Table 4, and no Elminae seem to be eaten though, as a group, these beetles are not rare.

Of the different types of food material utilized by the phytophagous species the moss *Fontinalis* would appear to be that which varies least in amount; the amount of detritus available probably varies with the rainfall and the season, and the supply of green algae undergoes the most marked fluctuation. The quantitative data given for the Tees by Butcher *et al.* (1937, pp. 70–1) show the violent fluctuations that may take place in the amount of algal growth on the bed of a rapid, stony river; thus on 9 September 1931 no *Ulothrix* was recorded, on 28 September the growth amounted to 119 per sq.mm., on 7 October this had diminished to 1 per sq.mm., and these tables furnish many more such examples. Observations on the gut contents of *Ephemerella* described in § 4 (*d*) suggest that *Ephemerella* feeds on *Ulothrix* when this is plentiful and turns to *Fontinalis* when the *Ulothrix*

is scarce, and it is possible that other species that feed on green algae have some standby to turn to when this is not available.

The role of the higher plants in the nutrition of fresh-water animals is discussed by Welch (1935, chap. 11). Shelford (1918, p. 47) considered that 'One could probably remove all the larger plants and substitute glass structures of the same form and surface texture without greatly affecting the immediate food relations'. Welch regards this view as not well grounded, and points out that there is evidence that the larger plants serve as food for many invertebrate species; that they are eaten only to a very small extent by the fishes is probably correct.

The results of this investigation do not seem to suggest that the diatoms form a very important part of the food of the fauna in spite of their abundance and variety. Of the species studied only *Philopotamus montanus* seems to be mainly dependent on them. However, it is possible that the very young stages of some species subsist to a considerable extent on diatoms. This, however, requires further investi-

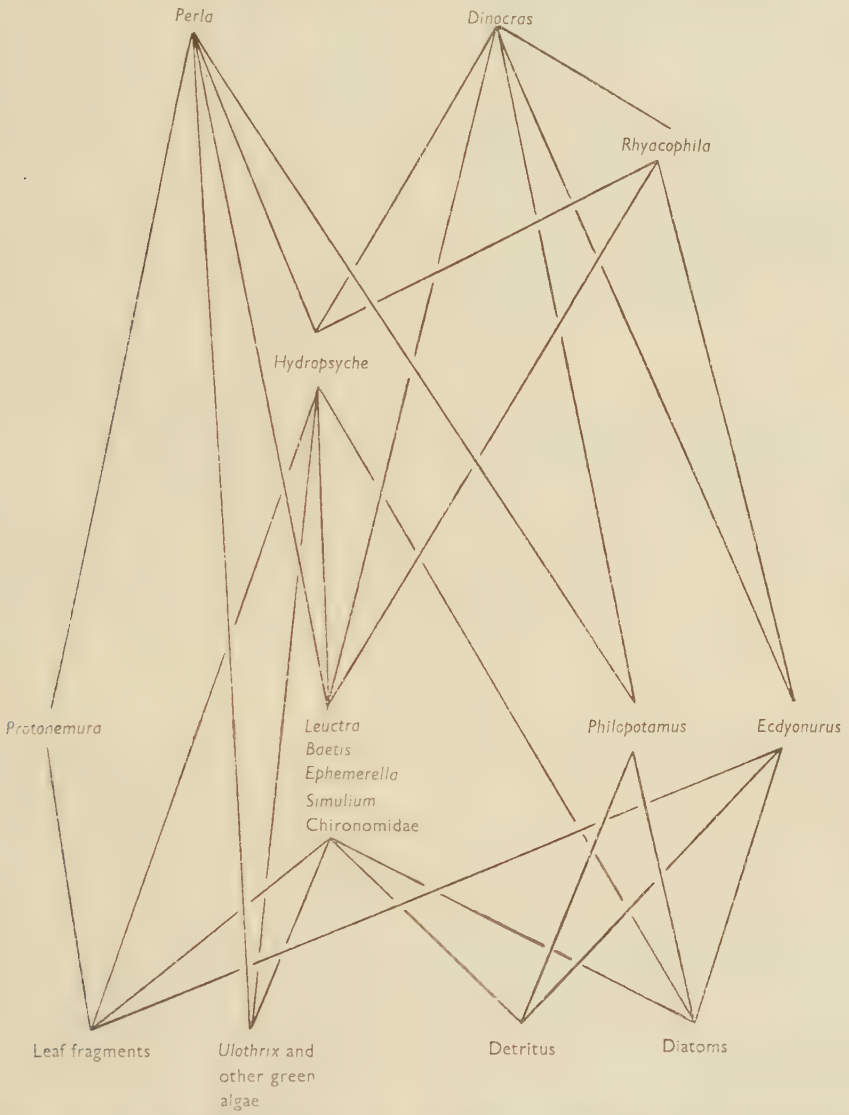

Fig. 2. The main features of the food chain in *Perla carlukiana*, *Dinocras cephalotes*, *Rhyacophila obliterata* and *Hydropsyche instabilis*. Based on Table 4 and, in the case of *Protonemura* and the Chironomidae, on the works cited in § 4 (*a*).

gation; in the case of the Plecoptera, Hynes (1941, p. 535) considers that the early stages feed mainly on detritus. Diatoms are probably an important food for the chironomid larvae; Needham & Lloyd (1916, p. 394) state that they are one of the chief foods of midge larvae, and it has been noted that the Chironomidae Orthocladiinae appear in the river Tees at the time of the spring diatom maximum (Butcher *et al.* 1937, p. 146).

From Table 4 it is possible to construct diagrams showing the food chain for the species investigated; Fig. 2 is an example summarizing the main features of the food chain in the case of *Perla*, *Dinocras*, *Rhyacophila* and *Hydropsyche*.

It would appear that further investigation on the lines of the present study should be of interest, and the writer hopes to carry out similar research on acid streams in the same area.

SUMMARY

1. This paper deals with the Sawdde and its tributary, the Clydach. These are swift, stony trout streams flowing on the northern side of a range of hills, and have cool, unpolluted, alkaline, moderately calcareous water, are very constant in flow and have a very stable bed.

2. The fauna of the Clydach has been described in a previous study. The fauna of the Sawdde, examined in July-September 1948, included about 75 species; dominant animals are *Atractides brevirostris*, *Perla carlukiana*, *Leuctra fusciventris*, *Ephemerella notata*, *Baetis rhodani*, *Glossosoma boltoni* and *Rhyacophila obliterata*.

3. The flora of the Sawdde and the Clydach is described. *Fontinalis antipyretica* is widely distributed and abundant at some points. *Ulothrix* is the dominant green alga. There is a rich diatom flora; characteristic species are *Diatoma vulgare*, *Ceratoneis arcus*, *Achnanthes* spp., *Cocconeis placentula* and *Navicula viridula*.

4. The food of the dominant insect species has been studied and about 600 specimens were examined for gut contents. *Perla carlukiana*, *Dinocras cephalotes*, *Rhyacophila obliterata* and *Plectrocnemia conspersa* are the chief predatory species; *Baetis*, *Ephemerella*, *Simulium* and chironomid larvae are their most frequent prey. The common mayflies are entirely herbivorous; *Baetis* feeds upon *Ulothrix* and other green algae, detritus and diatoms; *Ecdyonurus* mainly upon detritus; *Siphlonurus* upon the leaves of higher plants and detritus; *Ephemerella* upon *Ulothrix* and *Fontinalis*. *Ecdyonurus venosus* and certain other common animals in the stream system are apparently able to escape being eaten by the predatory Plecoptera and Trichoptera. Of the common, larger insects *Philopotamus montanus* is the only species mainly dependent on diatoms.

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SURVEY OF A MOORLAND FISHPOND

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(With Plates 7–9 and 5 Figures in the Text)

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1. INTRODUCTION

(*a*) *Object*

A biological survey of an artificial fishpond in the Lake District is described in the following pages. An essential preliminary is clearly a reliable species list. In many previous surveys no more than a generic name has been given to most of the insect nymphs and larvae; it is the belief of the present author that freshwater ecology has reached a stage where this practice is no longer of great value. Accordingly an effort has been made to identify all the species encountered in the present survey, and it has achieved a fair measure of, though not complete, success. Most of the insects have been bred out from nymphs or larvae, and emerging adults have been trapped in floating cages. No less than 15 authorities have been kind enough to identify specimens for me, and acknowledgement is made in due course.

Though the number is not as great as an accurate survey demands, quantitative samples provide the basis of the present findings.

The piece of water, Three Dubs Tarn, was not quite typical, since bone meal was added to it every second year, and this affected the flora and fauna to some extent. But most fishponds are interfered with, and in the present instance this disadvantage was outweighed by the advantage that the tarn owner gave us a free hand and allowed us to use his boat and his boat-house whenever we wished. I am deeply indebted to Mr M. Illingworth, and take this opportunity to thank him.

(*b*) *General features*

Three Dubs Tarn lies on Claife Heights, a low range of fells lying to the west of Windermere, at an altitude of about 700 ft. (215 m.). It was made in 1908 by the erection of a concrete dam. The name suggests that there were three pools originally, and it is probable that what is now the bottom of the tarn was formerly a bog at the head of the valley.

The tarn is surrounded by typical moorland vegetation growing on rather thin peat, and much of the area is covered with bracken (*Pteridium aquilinum*). There are also, as may be seen in Pl. 2, some larch trees, which have undoubtedly been planted.

Six streams flow into the tarn and, for present purposes, these have been numbered serially starting at the boathouse (see Figs. 1 and 2). The first is formed by two tributaries, one of which comes from a small well and the other from a small bog. The next two, some 250 and 350 yd. long respectively, are the largest. Both originate in bogs about 150 ft. above the level of the tarn and flow down a steep fellside. The last three come in on the west side and are quite tiny streams draining small bogs. The total drainage area is very roughly one-third of a square mile, which is quite small.

The surface area of the tarn is 3·966 acres (16,066 sq.m.). The depth contours of the tarn are shown on Figs. 1 and 2; it will be seen that generally the greatest depth is just over 3 m. or about 10 ft., though a channel near the outflow is a little more than 3·5 m. or between 11 and 12 ft. deep.

Table 1 shows the results of a chemical analysis made by Dr C. H. Mortimer in March 1937. He describes the water as clear, extremely poor in electrolytes, and high in dissolved organic matter. It is a typical soft moorland water. After the addition of bone meal later in 1937, the alkalinity rose to 19·5, but there was no change in the concentration of any other substance.

In 1947 and 1948, Mr F. J. Mackereth made a regular series of estimations of alkalinity and calcium. The alkalinity reached a maximum of 7·5 at the end of a long dry spell in August; a wet autumn brought it down to a minimum of 0·7, and it fluctuated round a value of about 2 throughout the winter. Calcium,

Table 1. *Water analysis, 24 March* 1937

	At the surface	At a depth of 2 m.
pH in the field	6·7	6·7
Turbidity, the amount of light passing through a sample as a percentage of the amount passing through distilled water	94·8	93·3
Nitrate as NO_3 (mg./l.)	0·1	0·1
Alkalinity as $CaCO_3$ equivalent (mg./l.)	2·94	2·78
Phosphate as P_2O_5 (mg./l.)	Less than 0·002	Less than 0.002
Nitrite as NO_2	None	None
Ammonia as NH_3 (mg./l.)	Less than 0·02	Less than 0·02
Silicate (mg./l.)	1·3	1·4
Oxygen absorbed from acid permanganate (mg./l.)	1·34	1·13

unexpectedly, varied less. The maximum, on 27 August was 5·2, and the minimum, on 26 February was 3·0 mg./l.

Table 2 shows the alkalinity and calcium concentrations for the six inflows and the outflow. In April the highest calcium concentration was nearly twice the lowest. There was a long fair spell in May and early June, but most of June was wet and cold. Early in July calcium and alkalinity values were higher than in April. The concentration in the well, which was one of the sources of stream 1, was unusually high for the Lake District.

Temperature was not measured regularly. The following isolated readings were recorded: 9 July, 14·9° C.; 27 August, 20·7 °C.; 3 September, 19·6° C. These were surface temperatures; the temperature in a stream issuing from a leak at the foot of the dam was usually about 0·3° C. lower than at the surface. The reading of 20·7° C. (69·3° F.) was obtained towards the end of an exceptional fine spell.

Typically the water-level of such a tarn remains very constant. There will be enough coming in in dry weather to keep a small flow of water over the sill of the dam, and after heavy rain water can escape readily so that the rise is no more than an inch or two. But the water of Three Dubs Tarn is used to drive a small electric installation at the owner's house. In 1947, the house was occupied throughout the summer for the first time, and the level twice fell considerably; it reached a point 18 in. below the overflow in mid-June, filled up again and reached the top of the outflow by the end of July, and then dropped to a level of 23 in. early in September. According to Mr Illingworth a big fall in the water-level had only happened once before.

Table 2. *Analysis of the streams entering Three Dubs Tarn*

	Alkalinity as $CaCO_3$ equivalent in mg./l.		Calcium as mg./l.	
Inflow number	15 April 1947	2 July 1947	15 April 1947	2 July 1947
1	10·2	28·6	6·4	12·3
Well	.	59·8	.	26·6
2	4·45	12·2	4·44	6·7
3	2·42	.	3·28	.
4	9·20	.	5·25	.
5	2·63	.	3·32	.
6	3·88	.	4·44	.
Outflow	3·00	.	3·24	.

It is convenient to retain certain names which were found useful during the field-work. The bay into which stream 1 flows is Boathouse Bay, and that receiving stream 6 is *Carex* Bay. When not otherwise qualified, the 'delta' refers to the convex stretch of shore immediately north of inflow 2.

(*c*) *History of the observations*

At the end of July 1936, several days were spent at the tarn by Mr K. R. Allen, Dr C. H. Mortimer, Dr M. Rosenberg, and the author. Prof. W. H. Pearsall gave assistance with the physiographical and botanical survey (Fig. 1). In subsequent years observations were made by the author, who visited the tarn in March and July, or at about those times, and obtained fauna samples from the mud and from the vegetation.

There was a gap from 1941 to 1947. During 1947 the author, assisted by Mr K. Shepherd, visited the tarn once every week. Two floating cages were put on the tarn at the beginning of the season, and sorting, labelling, and pinning the catch from them, which was much larger than expected (Tables 8–10), occupied a great deal of the available time. A few quantitative faunistic collections comparable with those of pre-war years were made, but it is a shortcoming of the study that most of the work on the bottom population was done at one time and all the work on the emerging insects at another. At present

the sorting of grab samples is a time-consuming process, and synchronous observations of the type described in subsequent pages are not within the scope of one worker and one assistant.

The weekly visits have continued up to the time of writing (June 1948), and Dr J. W. G. Lund and Mr F. J. Mackereth have examined the phytoplankton collections and the water samples respectively.

(*d*) *Methods*

Plankton was collected with a bolting-silk townet, samples of the bottom mud were collected with a Petersen Grab, and neither technique calls for comment.

For obtaining quantitative samples in the weeds a special grab was designed. It was a metal box enclosed by two fixed sides and two hinged sides. When the hinged sides were apart, the opening at the bottom of the box enclosed a square of fixed area—1 sq.ft. on a rough model in use before the war and $\frac{1}{10}$ sq.m. on the finished product turned out by the Wray Castle workshop in 1947. When the hinged sides were brought together, which was effected by means of two handles, the bottom was closed. The device is illustrated in Pl. 8. The upper picture shows the grab open and about to be placed over a suitable patch of vegetation, and the lower picture shows it closed with the water flowing out of the holes in the sides provided for the purpose.

It was assumed that the rarer animals in the tarn were so widely spaced that a grab sample would probably miss them, and accordingly at each visit, after one or two grab samples had been taken, collections with an ordinary pond-net were made. This assumption is examined in a later section and found to be false.

Although the hand-grab was designed to sample the fauna of the rooted plants, it also brought up the top inch or so of the substratum in which the plants were rooted. It was necessary, therefore, to sieve the samples and pick over by hand the debris left behind. This was a long and tedious process which usually took 6–8 hr., and so the number of samples which could be examined was small. Petersen Grab samples might take several days, as a great deal of vegetable debris was left behind after the fine particles had passed through the sieve. The finest sieve had 40 meshes to the linear inch.

Emerging adults were caught in a floating cage illustrated in Pl. 9 (Scott & Opdyke, 1941; Miller, 1941; Sprules, 1947). The cage itself fitted into a frame buoyed up by sealed tins or by corks. It consisted of a wooden frame with three sides and the top of celluloid, and one side of mosquito netting with a sleeve. The height was about 30 cm. and the bottom, which was of course open, was a square having an area of $\frac{1}{3}$ sq.m. The original idea was to lie alongside the cage in a boat, insert an arm through the sleeve, and catch the insects inside with a sucking-tube. This proved impracticable, and the technique eventually adopted was to lift the cage out of the frame, place it on a board, and remove it to a table in the boathouse. If the cage was tilted towards the window, the insects did not escape since they tended to fly towards the light, and they could be gathered with a sucking-tube.

There were two cages, one, cage *M*, being in the middle of the tarn, and the other, cage *S*, being near the side in shallow water over a thick bed of *Apium*. The original plan was to have one cage over vegetation and the other over bare mud, but *Nitella* had spread so much during the war interval that an area of bare mud in deep water could not be found in 1947.

The cage cannot be regarded as a quantitative instrument. The number of the dragon-fly *Enallagma cyathigerum* caught was influenced by whether or not the sleeve was hanging down in the water, and another common species, *Pyrrhosoma nymphula*, did not emerge in the cage at all.

(*e*) *Soils of the tarn*

The valley lies in the Bannisdale slate and the underlying rock is exposed in many places. Elsewhere it is covered by thin peat or boulder clay.

The bulge in the outline of the shore immediately to the north of inflow 2 is a delta. It appears to be rather large to have been brought down by so small a stream, and it may have been the result of the collapse of an ice dam further up when the last glaciation was withdrawing. Deposits of this type are frequent in the Lake District.

To-day there are a few bare rock faces, notably just north of the boathouse and off the point west of inflow 6 (Fig. 1), but the total area is small. North of the delta there is a stretch of stony shore; the stones lie in a well-defined zone and it looks as if man has had something to do with their being there.

Elsewhere in the shallow water the tarn is floored with a stiff black deposit. Analysis of four samples taken near the delta showed that the amount of organic matter, determined by combustion, was about 37%. The rest of the sample was probably boulder clay. At a depth of 1 m. off this shore, though at a greater depth off other shores, the bottom mud suddenly becomes more yielding, and the organic matter in two samples was about 58%. This soil is derived mainly from material washed in by the streams to judge from the debris left behind after sieving, and it contains more mineral matter than is usual in tarns of this type. At either end of the delta two patches of mud, into which the human leg sinks a long way, represent deep accumulations of vegetable remains; *Potamogeton natans* grows on both patches.

2. THE HIGHER PLANTS

Fig. 1 shows the vegetation as revealed by a 3-day survey at the end of July 1936. Perhaps the most striking thing about it is its paucity, rooted plants being almost confined to the neighbourhood of the stream mouths and the delta.

The area indicated by horizontal lines and designated bog may be ignored for the moment, and *Juncus effusus* and *J. articulatus* around the edge scarcely belong to the water community. True aquatic emergent plants are *Carex rostrata* and *Iris pseudacorus* at the extreme edge, and *Equisetum fluviatile* and *Typha latifolia* in somewhat deeper water. The commonest submerged plant of the shallow water is *Apium inundatum*. *Juncus bulbosus* forma *fluitans* (*'Juncus fluitans'*) and *Callitriche intermedia* occur in thick patches at several places, and *Sparganium minimum*, though not growing densely anywhere, is well scattered over the tarn.

The deeper water has a very poor flora except at the north end where there is a good patch of

Fig. 1. General features of Three Dubs Tarn and vegetation in July 1936.

Potamogeton natans. Elsewhere only a few plants of *Nitella translucens* and *Myriophyllum alterniflorum* are found.

Fig. 2 shows the vegetation in 1947. It is a composite map based on observations all through the in the deeper water there is a striking difference, for almost the whole area, formerly so barren, is now covered with *Nitella*. This plant was first obtained in Petersen Grab samples in the middle of the tarn in 1940, in which year and the following it occurred in

Fig. 2. General features of Three Dubs Tarn and vegetation in 1947.

summer and facilitated by the low water-level in August. It must be emphasized, when the two surveys are compared, that the later is a product of many more hours' observation and more favourable conditions.

There are no great changes in the shallow water, and much of the tarn is still without vegetation, but three out of seven samples. Apparently a sudden maximum was reached in 1944, for in that year the seine that had worked satisfactorily in previous years was badly tangled up with the weed. Mr G. Thompson, who was in charge of the seine netting, estimates that several cart-loads of *Nitella* were

Photo John Clegg

Photo 1. Three Dubs Tarn, looking over the tarn to the dam.

Photo John Clegg

Photo 2. Hand grab open and ready to go down.

Photo John Clegg

Photo 3. Hand grab closed with sample, water draining off.

brought to the bank. Subsequently, a seine of larger mesh was used. Since 1944, *Nitella* has been less thick, but in 1947 it formed a fairly uninterrupted sward. The development of this plant is perhaps connected with the dressing of the tarn with bone meal.

Isoetes lacustris occurs at intervals in the deeper water, and there is a good sward of it off the boathouse. It is more likely that it was missed in the 1936 survey than that it has established itself in the tarn since then. The patch of *Potamogeton natans* towards the north end of the tarn is smaller in 1947, doubtless because it has been cut every year. The species has, however, established itself in inflow 1 bay, where it was first noticed in March 1941, and at the north end of the delta.

In the shallower water it is surprising to find one new species, *Littorella uniflora*, in no less than eight places, at each of which it forms a compact sward. In boathouse bay the sward has certainly grown in extent during the years of observation, and probably *Littorella* has spread in other parts of the tarn as well. But it seems unlikely that this species was totally absent from the tarn in 1936.

The distribution of the species off the delta is not identical in 1936 and 1947. This stretch of shore has been kept under closer observation than any other, and the notes indicate that there has been considerable fluctuation from year to year.

In 1936 and 1937 the vegetation was similar, but in 1938 both *Callitriche* and *Juncus bulbosus* forma *fluitans* had disappeared. In 1939 there was a patch of *Callitriche* at the north end in March, but it had disappeared in July. *Juncus bulbosus* forma *fluitans* was present in July. In August 1940 both species were present in fair quantity and *Sparganium minimum* occurred all along the east side of the tarn. In March 1941, *Juncus bulbosus* forma *fluitans* had disappeared again. Observations were then interrupted until 1947.

There is more *Equisetum* in 1947, but the *Typha* has died out in the deeper water, and the patches on both sides of the tarn have shrunk. The old dead stems in the deeper water can still be seen. The plant, which is scarcely to be expected at all in such a base-deficient place, does not flourish apparently, and in 1947 there were only four flowering heads in the patch in inflow 6 bay.

From a study of neighbouring tarns it is possible to forecast the future sequence of events in Three Dubs Tarn. *Potamogeton natans* will gradually cover the open water, and then, having reached a peak, will be forced into an ever-decreasing compass as *Carex* advances from the edge of the tarn, and perhaps from shallow islands in the middle as well. The total number of species will become fewer and fewer, as *Potamogeton* advances, but a certain number of bog species will come in with the encroaching *Carex*. Man influences this evolution, though whether he deflects the succession or merely retards it cannot be stated at present, but the latter alternative is the more likely. Cutting the *Potamogeton natans* keeps the tarn in an open condition for much longer than if there were no interference, but eventually man gives up the struggle against the vegetation, and the tarn is neglected. Usually the dam falls into a state of disrepair with a consequent drop in the water-level, and the result of this is an acceleration of the rate of development of swamp conditions.

Finally there is the bog, which has been excluded from the foregoing discussion because no detailed floristic survey was made of it in 1936. There are small patches on either side of inflow 3 and larger patches on either side of inflow 2. The more southerly of these latter is shown larger in Fig. 2 than in Fig. 1, but I have the impression that the original survey dismissed the bog as marginal vegetation and did not map it with sufficient accuracy to make strict comparison in 1947 justified.

The largest piece of bog is north of inflow 2 and nearly all the observations on this type of community have been made here. *Sphagnum* grows over the whole of it, and towards the tarn there is a thick growth of *Juncus effusus*, which at the north end is partially replaced by *Carex rostrata*. Towards the land there are zones of *C. canescens* and *C. nigra*, both of which are less abundant than the first two species mentioned. Other plants are *Iris pseudacorus*, *Galium palustre*, *Hydrocotyle vulgaris*, *Caltha palustris*, and *Comarum palustre*. *Eriophorum angustifolium* was found only on the piece of bog to the south of inflow 2.

A few pools of open water stand in the bog, but a person walking across it will create a small expanse of water at every footstep.

3. ANIMALS FOUND

The tarn can be divided into five major habitats: the surface, the rooted plants, the bottom mud, the bog, the open water.

(*a*) *Surface fauna*

The surface fauna is poor; *Gerris* occurs in rather small numbers in the bays and *Microvelia* in the thicker emergent vegetation. No Gyrinidae have ever been seen on the tarn. Nearly all the pond skaters are *Gerris lacustris* (Linn.), though *G. odontogaster* (Zett.) has been taken once. Of the three British species of *Microvelia*, *M. reticulata* Burm. is the only one recorded from the Lake District.

(*b*) *Weed fauna*

The animals caught in the weeds are set out in Table 3. The numbers refer to catches made with the

Table 3. *Weed Fauna*

		9 collections in March			16 collections in July and August		
		Total specimens	No. of hauls in which collected	Av. per haul	Total specimens	No. of hauls in which collected	Av. per haul
PLATYHELMINTHES:							
Tricladida	*Polycelis* sp.	.	.	.	.	.	.
Rhabdocoelida		.	.	.	.	.	.
POLYZOA							
Annelida		.	.	.	.	.	.
Hirudinea	*Herpobdella octoculata* (L.)	.	.	.	12	2	0·7
	Helobdella stagnalis (L.)	.	.	.	.	.	.
	Protoclepsis tesselata (Müll.)	.	.	.	.	.	.
	Glossosiphonia sp. juv.	.	.	.	.	.	.
	Indet.	3	2	0·3	21	7	1·3
MOLLUSCA	*Limnaea pereger* (Müll.)	1	1	0·1	8	3	0·5
	Ancylastrum fluviatile (Müll.)	.	.	.	.	.	.
HYDRACARINA	*Limnochares aquaticus* (Linn.)	.	.	.	1	1	0·06
	Diplodontus despiciens (Müll.)	.	.	.	.	.	.
	Limnesia maculata (Müll.)	.	.	.	.	.	.
	L. connata Koen	1	1	0·1	.	.	.
	Frontipoda musculus (Müll.)	.	.	.	.	.	.
	Piona carnea (Koch)	.	.	.	1	1	0·06
	Hydrochoreutes ungulatus (Koch)	.	.	.	2	1	0·1
	Forelia liliacea (Müll.)	3	1	0·3	1	1	0·06
	Midea orbiculata (Müll.)	.	.	.	1	1	0·06
	Mideopsis orbicularis (Müll.)	.	.	.	.	.	.
	Arrhenurus ornatus George	1	1	0·1	4	1	0·3
	A. leuckarti Piers.	.	.	.	1	1	0·06
	A. neumani Piers.	.	.	.	18	1	1·1
	A. robustus Koen.	.	.	.	.	.	.
	A. virens Newm.	.	.	.	2	1	0·1
	Arrhenurus indet.	6	4	0·7	.	.	.
	Indet.	6	1	0·7	36	6	2·3
	Nymphs	1	1	0·1	6	2	0·4
CRUSTACEA:							
Decapoda	*Gammarus pulex* (L.)	18	1	2	3	2	0·2
Copepoda	*Canthocamptus staphylinus* (Jurine)	.	.	.	.	.	.
	Cyclops albidus Jurine	.	.	.	.		.
	C. agilis speratus Lilljeborg	.	.	.	.	.	.
	C. viridis (Jurine)	.	.	.		.	.
Ostracoda	*Cypricercus obliquus* (Brady)	.	.	.	.	.	.

Cladocera	*Eurycercus lamellatus* (Müll.)	.	.	.	.	.	.
	Chydorus ovalis Kurz	.	.	.	.	.	.
	C. sphaericus (Müll.)	.	.	.	.	.	.
INSECTA:							
Plecoptera	*Nemoura variegata* (Olivier)	6	2	0·7	.	.	.
Ephemeroptera	*Leptophlebia marginata* (L.)	242	9	27	.	.	.
	L. vespertina (L.)						
	Cloëon simile Eaton	.	.	.	.	.	.
Odonata	*Pyrrhosoma nymphula* (Sulz.)	29	7	3·2	97	12	6·0
	Enallagma cyathigerum (Charp.)						
	Lestes sponsa (Hansem.)						
	Sympetrum scoticum (Don.)	.	.	.	9	8	0·6
	Aeshna juncea (L.)	.	.	.	6	4	0·4
Hemiptera	*Corixa scotti* (D. & S.)	186	9	21	51	9	3·2
	C. castanea (Thoms.)	1	1	0·1	6	3	0·4
	C. distincta (Fieb.)	16	4	1·8	8	2	0·5
	Corixa nymphs	.	.	.	161	15	10·0
	C. punctata (Illig.)	.	.	.	.	.	.
	C. fossarum Leach	.	.	.	.	.	.
	C. striata (L.)	.	.	.	.	.	.
	C. praeusta (Fieb.)	.	.	.	1	1	0·06
	Cymatia bonsdorffi (Sahlb.)	.	.	.	.	.	.
	Notonecta obliqua obliqua Gall.	.	.	.	.	.	.
Trichoptera	*Phryganea varia* Fab.	.	.	.	8	4	0·5
	Limnophilus marmoratus Curt.	30	4	3·3	11	7	0·7
	Leptocerus aterrimus Steph.	.	.	.	27	7	1·7
	Triaenodes bicolor (Curt.)	7	1	0·8	11	5	0·7
	Cyrnus trimaculatus (Curt.)	9	4	1·0	3	3	0·2
	Oxyethira costalis (Curt.)	.	.	.	.	.	.
	Indet.	19	5	2·1	1	1	0·06
Coleoptera	*Haliplus fulvus* (Fab.)	.	.	.	6	4	0·4
	H. ruficollis (Deg.)	.	.	.	.	.	.
	Haliplus larvae	.	.	.	6	2	0·4
	Deronectes duodecimpustulatus (Fab.)	1	1	0·1	2	2	0·1
	D. depressus (Fab.)	1	1	0·1	1	1	0·6
	Deronectes larvae	.	.	.	1	1	0·6
	Donacia type pupae	.	.	.	4	1	0·3
Diptera	Chironomidae	.	.	.	.	.	.
	Anopheles maculipennis Meig.	.	.	.	.	.	.
	Tabanidae larvae	2	2	0·2	.	.	.
AMPHIBIA	*Triturus vulgaris vulgaris* (L.)		.	.	5	2	0·3
	T. helveticus helveticus (Raz.)						
	Triturus tadpoles	.	.	.	3	2	0·2
	Rana temporaria temporaria L.	.	.	.	.	.	.
	Bufo bufo bufo L.	.	.	.	.	.	.

Table 4. *Insects, excluding Diptera, caught in the two floating cages in* 1947*: S, the cage over shallow water near the side of the tarn; M, the cage over deep water in the middle*

		May			June				July					Aug.				Sept.				Oct.	Total in cage	Total in cage
		15	21	29	5	11	18	25	2	9	16	23	30	6	13	20	27	3	10	17	24	1	*S*	*M*
Ephemeroptera	*Leptophlebia marginata*	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	0
	L. vespertina	.	.	3	.	.	1	4	1	.	.	1	.	.	.	.	.	.	.	.	.	.	7	3
	Cloëon simile	.	.	.	6	2	1	1	1	.	.	.	1	3	1	2	5	2	1	1	.	2	8	21
	Above not separated	.	.	.	10	.	.	15	4	.	1	.	.	2	3	5	.	.	.	.	.	.	16	24
	Caenis horaria (L.)	.	.	.	.	.	.	1	14	2	8	10	5	1	.	1	.	.	.	.	.	.	0	42
Odonata	*Enallagma cyathigerum*	.	.	.	9	9	9	2	14	5	2	.	1	.	.	.	.	.	.	.	.	.	44	7
Trichoptera	*Cyrnus trimaculatus*	.	.	.	3	2	1	.	1	.	1	1	1	2	.	.	.	.	.	.	.	.	3	9
	Oxyethira costalis	.	.	.	.	7	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	9
	Leptocerus aterrimus	.	.	.	.	.	.	.	.	.	2	.	.	.	1	.	.	.	.	.	.	.	2	1
	Phryganea varia	.	.	.	.	.	.	.	1	.	.	.	1	2	1	.	2	.	.	.	.	.	2	5

Table 5. *Catches of* Corixa *species at different stations in Three Dubs Tarn*

	Boat-house bay	*Carex* near inflow 6	*Apium*, etc. off the delta	Bog	Total
C. scotti	1610	314	282	33	2239
C. castanea	0	2	25	46	73
C. distincta	48	1	2	0	51

hand grab at two times of the year, in March, and in late July or August. The species with no numbers were scarce, and were taken only in net collections, in grab samples in other months, or by other means. The names of Plecoptera, Ephemeroptera, Odonata and Trichoptera are based on catches in the floating cages (Table 4) and on the results of rearing in the laboratory.

The quantitative collections were made in the 6 years from 1936 to 1941, and also in 1947 in *Apium*, *Callitriche*, *Juncus bulbosus* forma *fluitans*, and *J. effusus*; but no significant differences from year to year or from plant to plant are apparent, presumably because the number of samples was too small.

Table 4, based on the catches in the floating cages, shows the emergence seasons.

A single specimen of a *Polycelis* (Platyhelminthes),

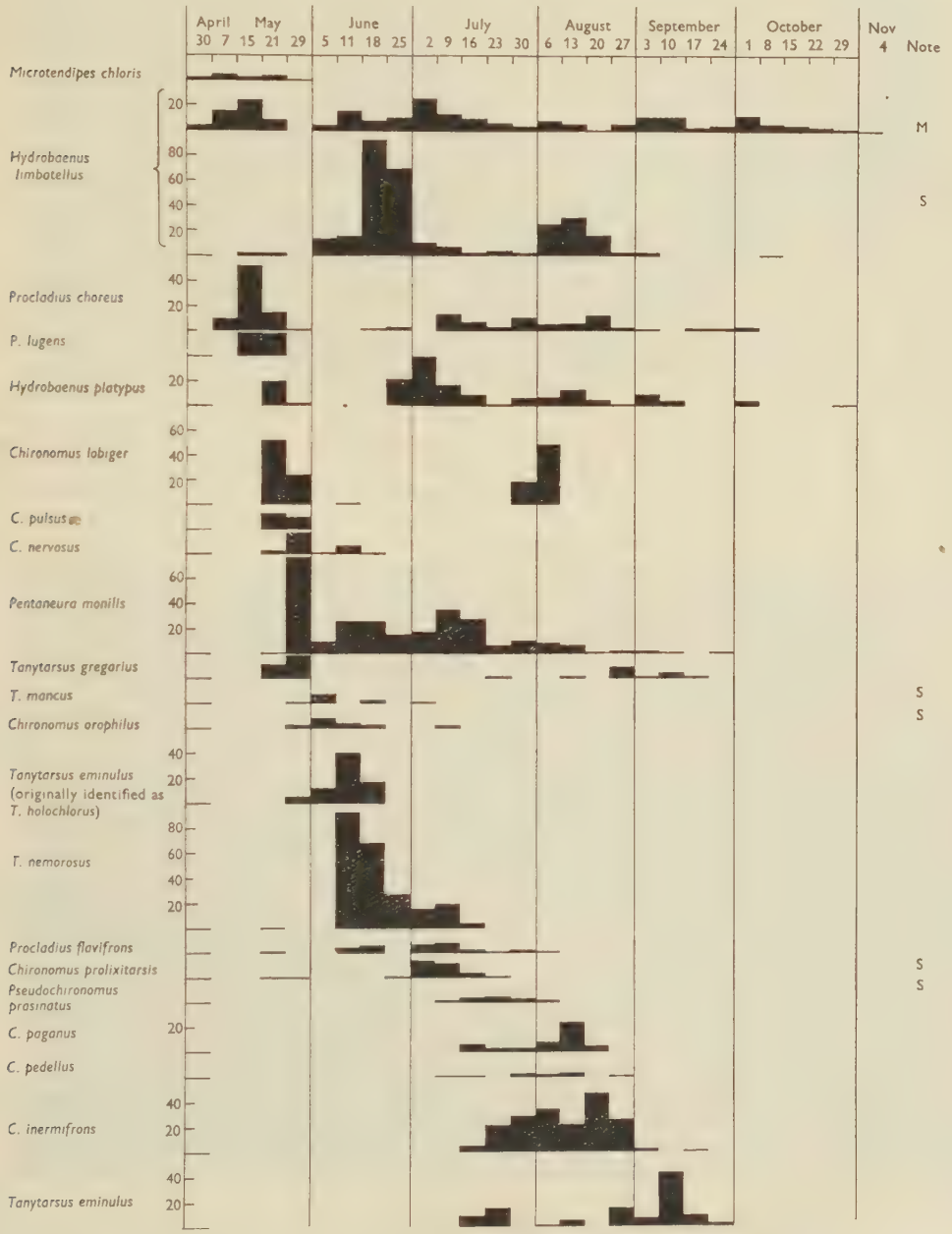

Fig. 3. Emergence of the commoner Chironomidae in 1947 (Tables 8 and 9).

of which the specific identity is discussed in the next section, was taken off the bog, from which it had probably strayed since it was common there. The Polyzoa, which were not named, were found attached to the frame of one of the floating cages.

Hirudinea are scarce, at least when comparison is made with other waters. Most of the specimens were identified by the present author as *Herpobdella octoculata*. *Helobdella stagnalis* was encountered twice, on both occasions in deep water. On the first a single specimen was brought up with a mass of *Nitella* on a plant grab, and on the second four were found clinging to the stone by which the cage was moored. Single specimens of *Protoclepsis tesselata* have been taken twice and a single specimen of a *Glossosiphonia* too small to name once.

Ancylastrum fluviatile (Mollusca) is found on the dam in some numbers, though it has not been found on any of the exposed rock faces or on the stones.

A single catch of 18 *Gammarus pulex* (Crustacea) in one grab haul in March 1939 was quite exceptional. The sampling place on this occasion was opposite the stream mouth, and the shrimps may have come down from the stream where they were always more abundant. Smaller Crustacea taken from the weed samples were not counted, since the grab was not designed to retain organisms of this size at that time. The collecting technique did not differentiate between true planktonic species and weed dwellers.

Nemoura variegata (Plecoptera) occurred among *Juncus* and *Carex* at the edge of the tarn, and a few specimens were taken in the weeds.

Nymphs of *Leptophlebia* (Ephemeroptera) were the commonest animals in the spring grab collections, and both British species occurred, *L. vespertina*, it would appear from Table 4, being the commoner. No difference in the habitat of the two species was noted. The young nymphs appear in September or October. There is evidence from here (cf. last two columns of Table 4) and from elsewhere that *Cloëon simile* inhabits weed in relatively deep water. It is thought that this species increased greatly in numbers during the war, as *Nitella* spread over the tarn, and that this accounts for the discrepancy between adult numbers (Table 4) and nymphal numbers (Tables 3 and 7).

It is not known why *Pyrrhosoma nymphula* (Odonata), a common species in the tarn, did not emerge in the floating cages. Large numbers of nymphs were found crawling up the stone walls of the boat-house to metamorphose. In 1947, an exceptionally late season, adults did not appear till the latter half of May, a month later than is usual in the district. *Enallagma cyathigerum* was another common dragon-fly.

Lestes sponsa is numerous in Lake District tarns, more so in most than in Three Dubs. It must spend the greater part of its life buried in the mud for, from August to May inclusive, it is never found in pond-net collections. Quite suddenly in June nymphs appear, most of them fully grown. Adults are on the wing soon afterwards and by the end of July only an occasional nymph is to be found.

The large dragon-flies have a similar life history, for, though none of them have been taken in the spring collections, they occur regularly in the summer collections, but the period when they may be found among the weeds is longer. *Sympetrum scoticum* first appeared in June in 1947, and specimens were to be seen flying over the tarn up till early October; on another tarn a specimen was seen on 21 October.

All the specimens of the genus *Aeshna* examined proved to be *A. juncea*, though, since *A. cyanea* (Müll.) breeds elsewhere in localities of the same type, it would be rash to state categorically that it does not occur in Three Dubs Tarn.

A cast skin of *Cordulegaster boltonii* (Don.) was found beside the tarn near inflow 2, but the nymph almost certainly came from the stream and not from the tarn.

In pond-net collections Corixidae, order Hemiptera, are the most abundant animals in the shallow water. Table 5, which includes the bog, although the fauna of this part of the tarn has not so far been mentioned, shows the three common species and the places where they have been found. *Corixa scotti* is by far the most abundant species and only in the thick vegetation of the bog, where *C. castanea* is commoner, does it take second place to any other species. These are two good indicator species, typical of base-deficient barren conditions. As the reed beds extend it is to be expected that *C. castanea* will become more important. Out of a total of 51 *C. distincta* (Fieb.), 48 were taken in Boathouse Bay, that is off the mouth of the stream with a calcium concentration distinctly higher than that of any of the others. This is what might be expected from what has been observed elsewhere (Macan, 1938).

Not a single Corixid, adult or nymph, has been taken by the Petersen Grab from the deeper water (Table 7). In August 1947 collections designed to discover their depth limit showed that these creatures did not occur where there was more than about $2\frac{1}{2}$ ft. (75 cm.) of water from the surface to the top of the mud. The height of the vegetation did not seem to have any effect.

During the whole of the observations only three specimens, two nymphal and one adult, of *Notonecta* were taken. All were secured with a net. The adult was *N. o. obliqua*.

The grab, as explained, brought up some bottom mud with each sample, but, as the amount was variable, there was no point in counting the animals in it. Chironomidae (Diptera) are common to the

Photo John Clegg

Photo 4. Close-up view of floating cage and supporting frame.

Photo John Clegg

Photo 5. Floating cage.

weeds and to the mud, but no separation of the specimens from the two habitats was possible, and therefore it has been necessary to omit the chironomids from Table 3.

On 3 September 1947 five pupae and one larva of the mosquito *Anopheles maculipennis* were found in the *Apium* off the delta. On this date, the water-level being abnormally low, much of the *Apium* was floating at the surface and so providing the *Anopheles* with cover which would not otherwise have been present. This species is scarcely typical of Three Dubs, though it occurs in the marginal *Carex* zone of Lake District tarns which have reached a more advanced stage of development.

Frogs and toads (Amphibia) came to the tarn to breed and both laid a good deal of spawn each year, the frogs in shallow places such as the bog, the toads in deeper water. Tadpoles disappeared rapidly and within a month there was never a single one to be found, though what preyed on them was not discovered.

(*c*) *Bog fauna*

Unfortunately the bog was dry for two periods during the summer of 1947, the year devoted particularly to filling up gaps in the species list, and so the records are somewhat incomplete.

Thorough collections were made in July 1936, March and July 1937, and January 1938, and it was found that the fauna differed quite considerably from that in other parts of the tarn. Taking the groups in the same order as in Table 3, leeches were scarce, and only a single specimen, which was not named, was taken. The mollusc fauna was quite different; *Limnaea pereger* did not occur at all; *L. glabra* (Müll.), a species typical of such places in the Lake District, was taken in fair numbers; and *L. palustris* (Müll.) was also recorded. Both species appear to have died out later. *Pisidium* was numerous, but *P. cinereum* Alder and *P. obtusale* Jenyns were the only species. Mites were rather scarce, and there were but two species, *Arrhenurus neumani* and *Diplodontus despiciens*. *Gammarus* was not found, nor was *Cloëon*, but *Leptophlebia* was abundant, though whether both species were present was not discovered. *Nemoura variegata* was more abundant than elsewhere in the tarn. *Lestes* was not recorded but the other Odonata were almost certainly the same as in the rest of the tarn. The corixids have already been discussed (see Table 5) and the Coleoptera are postponed to the end. Three of the *Trichoptera* were absent, but the other three, *Limnophilus*, *Triaenodes* and *Phryganea*, were present, though it is not certain that the species were the same. Newt tadpoles occurred.

Three groups rare in, or absent from, the rest of the tarn were Platyhelminthes, Tipulidae and Dixidae. The single representative of the first group was identified by the author as *Polycelis nigra* (Ehrenb.), but a specimen recently submitted to Dr T. B. Reynoldson was determined by him as *P. tenuis* Ijima. Other specimens from a similar tarn were all this species, which had not previously been recognized from Britain (Reynoldson, 1948), and it may be the only species to occur in such places. It appears to have been a fairly constant inhabitant of the bog, though its numbers have fluctuated considerably; it has been numerous on some occasions, but when in 1948 a good sample was required for Dr Reynoldson only a single specimen could be found, though this may have been an effect of the drying up of the year before.

Tipulidae, which emerged in May and June 1946, were identified as *Prionocera turcica* (Fab.), but since other species from similar places nearby have been reared at other times of year, this is probably not a complete list. Larvae of *Dixa* are abundant, and some specimens reared early in 1948 were all *Dixa aestivalis* Meig., but again it may be that other species occur at other times of the year and the possibility that the drying up in 1947 had some effect cannot be ruled out.

The minute water-bug, *Microvelia reticulata*, abounded on the surface of the water.

Finally there are the beetles, the group in which the greatest difference between the bog and the rest of the tarn was noted. Table 6 shows the results of collections made from 1936 to 1940. Beetles are abundant and there are many species. During the 4 years of the observations the composition of the population remained remarkably constant. Poor catches at the beginning were almost certainly due to the fact that the exact place to find the beetles had not been discovered; they were to be found in the pools which gathered round the collector's boots, but not in the pools which were always open.

The bog fauna may be summarized as a depauperate tarn fauna plus a wide and varied beetle fauna, *Limnaea glabra*, *Polycelis tenuis*, tipulid larvae, and dixid larvae. The abundance of *Pisidium cinereum* and *P. obtusale* was also characteristic.

When the bog pools filled again as the tarn level rose in July 1947, larvae of the mosquito, *Aëdes punctor* Kirby, were found, but their presence is attributable to the drying up, since the females oviposit on damp ground, and this species cannot be counted as a normal inhabitant of the habitat.

(*d*) *Mud fauna*

Table 7 presents the results of the Petersen Grab hauls made between 1936 and 1941 at two stations, both of which lay on a line from a point midway between inflow 5 and inflow 6 across to the middle of the delta. Station P was about one-third of the way

across from the east shore, and station 12 about a quarter of the way across from the west shore.

In July 1940 and March 1941 the grab struck a patch of *Nitella* and caught a number of animals not usually found, notably coenagriids in fair numbers, a few *Sympetrum* and various Trichoptera. These are weed dwellers which can evidently extend into the deeper parts of the tarn where conditions are suitable. It is noteworthy that the two most abundant members of the shallow-water fauna, the corixids and *Leptophlebia*, did not extend into deep water, and no *Aeshna* or *Limnophilus* were taken by the Petersen Grab.

Cyrnus, a caseless Trichopteron belonging to the family *Polycentropidae*, is widespread in the tarn and apparently not confined to places where plants grow. *Chaoborus*, the phantom larva, in some lakes leads a planktonic existence by night but lurks in the mud by day. A possible explanation of the unexpected absence of *Cloëon* has already been put forward.

The remaining animals are the true mud dwellers. *Caenis horaria*, the only Ephemeropteron, was quite numerous in 1938 and 1941, and again in 1947 to judge from the cage catches, but in all the other years only a single specimen was taken. The reason is not known. Table 4 shows that its season lasted from the end of June to the beginning of August.

Sialis lutaria (L.) (Neuroptera), and *Lumbriculus variegatus* Müll., apparently the only oligochaete, call for no comment.

Mideopsis orbicularis was the commonest of the mites, and, as only two examples were found in the weeds in shallow water, it would appear to be a species of the bottom mud. Others taken were *Arrenurus neumani*, *Forelia liliacea*, *Midea orbiculata* and *Piona variabilis* (Koch). A number of indeterminable nymphs of *Piona* were taken both in spring and summer. Only two specimens of this genus were taken in the weeds, but two mites caught in the plankton net both belonged to it.

Altogether seven species of *Pisidium* were found in Three Dubs Tarn. *P. nitidum* Jenyns, *P. hibernicum* Westerlund, *P. lilljeborgii* Clessin, and *P. milium* Held, were taken only in the mud in the deeper parts of the tarn. *P. cinereum* Alder occurred here, in the shallow water, and in the bog. *P. obtusale* (Lam.) and *P. personatum* Malm. were both found in the bog and the former in the *Carex* near inflow 6 as well.

The species of chironomid could be ascertained only from the catches in the cages. Tables 8 and 9 show in detail the captures of the commoner Chironomidae and other Diptera in cage *S* and cage *M* respectively, and Table 10 shows, in a more condensed form, the captures of the less common species in both cages.

Table 6. *Net collections of Coleoptera from the bog.*

		Spring collections				Summer collections				
		24. iii. 37	25. i. 38	18. iv. 40	26. iii. 41	31. vii. 36	7. vii. 37	2. viii. 38	26. viii. 39	28. vii. 40
Haliplidae	*Haliplus fulvus* (Fab.)	1	.	.	.	2	.	1	.	1
Dytiscidae	*Hydroporus tristis* (Payk.)	10	.	19	20	.	.	19	12	4
	H. umbrosus (Gyll.)	1	.	3	.	.	.	1	.	.
	H. gyllenhalii Schiodte	11	4	15	3	.	.	8	6	11
	H. palustris (L.)	.	.	.	.	2	.	.	.	.
	Agabus affinis (Payk.)	4	2	9	2	.	.	3	3	7
	A. sturmii (Gyll.)	.	.	1	1	.	.	2	.	1
	A. bipustulatus (L.)	.	.	.	.	.	.	1	.	.
	Ilyius fuliginosus (Fab.)	.	.	.	.	1	.	1	.	1
	Rantus exsoletus (Forst.)	.	.	1	.	.	.	.	.	.
	R. bistriatus (Bergs.)	.	.	.	.	.	1	.	.	.
Hydrophilidae	*Hydrobius fuscipes* (L.)	.	.	1	.	.	.	.	.	.
	Anacaena globulus (Payk.)	.	3	1	2	.	.	.	.	1

Fig. 3 presents the data for the commoner species in the form of histograms; most of them are taken from cage *M*, but some from cage *S*, and occasionally they are taken from both if there are marked differences. From these histograms the emergence times can be seen at a glance; there is great variation from species to species and no generalizations seem to be warranted.

The totals for both cages are shown in both Tables 8 and 9. The difference between the two is so great for many species that it must indicate an ecological difference, but beyond that no more can be said. As already noted, the original intention to separate mud dwellers and weed dwellers was not possible on account of the spread of *Nitella* during the war years.

Some unidentified specimens not shown in the tables bring the total number of species to 50, and it is interesting to speculate whether each of these manages to find a peculiar ecological niche, and, if so, where in what appears to be a rather uniform habitat. But,

Table 7. *Collections with the Petersen Grab from two stations near the middle of the tarn*

	Spring collections									
	Station P					Station 12				
	24. iii. 37	16. ii. 38	15. iii. 39	25. iii. 40	17. iii. 41	24. iii. 37	16. ii. 38	15. iii. 39	25. iii. 40	17. iii. 41
Chironomids	25	879	333	471	594	2	170	296	671	678
Ceratopogonids	4	4	8	9	9	.	1	.	2	2
Pisidium	12	86	78	168	355	1	7	6	122	197
Oligochaeta	3	12	6	11	6	1	.	3	7	.
Sialis	.	3	3	1	8	.	5	3	2	7
Hydracarina	.	.	1	7	3	.	16	17	16	9
Caenis	.	69	.	.	158	.	7	.	.	152
Leptocerus	.	1	.	.	.	.	.	.	.	2
Cyrnus	1	12	3	.	28	.	.	.	1	.
Phryganea	.	.	.	.	1	.	1	.	.	.
Triaenodes	.	.	.	.	2	.	.	.	1	.
Indet. Trichoptera	.	.	1	2	.	.	.	.	.	.
Chaoborus	.	.	.	.	.	.	1	.	.	.
Leptophlebia	.	1	.	.	.	.	.	.	.	.
Sympetrum	.	1	.	.	1	.	.	.	.	.
Coenagriids	.	.	.	.	28	.	.	.	.	.
Limnaea pereger	.	.	.	.	3	.	.	.	.	.
Total	45	1068	433	669	1196	4	208	325	822	1047
Vegetation	Nil.	Nil.	Nil.	Nil.	much *Nitella*	Nil.	Nil.	Nil.	some *Nitella*	Nil.

	Summer collections									
	Station P					Station 12				
	7. vii. 37	10. viii. 38	18. viii. 39	23. vii. 40	23. vii. 40	31. vii. 36	7. vii. 37	10. viii. 38	19. vii. 39	23. vii. 40
Chironomids	55	139	271	115	113	26	40	30	255	224
Ceratopogonids	1	1	1	.	5	3	1	.	1	3
Pisidium	14	138	63	186	130	4	.	27	27	124
Oligochaeta	2	6	17	4	13	1	.	.	6	3
Sialis	5	2	5	4	2	4	4	6	.	7
Hydracarina	1	.	.	4	2	.	2	8	6	2
Caenis	.	.	.	.	.	.	.	.	1	.
Leptocerus	.	.	.	5	.	1	.	.	.	1
Cyrnus	.	.	7	8	2	.	.	.	4	1
Phryganea	.	.	.	3	.	.	.	.	.	.
Chaoborus	.	.	.	.	.	.	1	.	.	.
Sympetrum	.	.	.	2	.	.	.	.	.	.
Coenagriids	.	1	.	15	.	.	.	.	.	.
Haliplus larva	.	.	.	.	1	.	.	.	.	.
Total	78	287	364	346	268	39	48	71	300	365
Vegetation	Nil.	Nil.	Nil.	much *Nitella*	Nil.	Nil.	Nil.	Nil.	Nil.	Nil.

since no attempt to associate larvae with known adults has been made, no contribution towards a solution of this problem has been possible. Miller (1941), working on the Chironomidae of a lake in Canada, points out that different species may be active over different ranges of temperature.

I learn from Mr Paul Freeman, to whom I am greatly indebted for the identification of the specimens, that the following are groups of closely related species: *Chironomus* (*Microtendipes*) *chloris* and *pedellus*; *Procladius lugens* and *flavifrons*; and *Chironomus* (*Chironomus*) *lobiger*, *pulsus*, and *nervosus*. Both species of the subgenus *Microtendipes* are more abundant in cage *M* than in cage *S*, but the two are well separated in time, *chloris* being one of the first species to appear and *pedellus* one of the last. Similarly, the two species of *Procladius* are commoner in the same cage but have different times of emergence, though the period separating them is not as great as in *Microtendipes*. Of the three species of *Chironomus*, *lobiger* is the only one to have two periods of emergence and *nervosus* is the only one which is not much more abundant in cage *M* than in cage *S*. These biological findings would seem to confirm the conclusions of the taxonomists that, though the species are not very dissimilar, they are distinct. On the other hand, in one species, there may be differences between specimens emerging at different times of year. Originally it was thought that both *Tanytarsus eminulus* and *T. holochlorus* were present, and the two emerged at different times of year; the original identifications have been retained in the tables and in Fig. 3 to illustrate this point. It is now thought that all the specimens are referable to *T. eminulus*, which is, therefore, a species with early summer forms differing slightly from the late summer forms.

(*e*) *Fauna of the open water*

The only species of fish is the trout, *Salmo trutta* L., but, as it is to be the subject of a separate paper, it may be ignored here. The plankton, therefore, remains. The zooplankton has received least attention of all the faunal groups, and only random records are available. In July 1936, Dr C. H. Mortimer found that *Diaptomus gracilis* Sars made up about 90% of the zooplankton, and the only other species present were *Diaphanosoma brachyurum* (Lieven) and *Ceriodaphnia reticulata* (Jurine). In June 1947, *Diaphanosoma brachyurum* was the commonest species in the plankton. In March 1941, Mr D. J. Scourfield recorded *Diaptomus gracilis*, *Cyclops agilis speratus*, *C. viridis* and *Canthocamptus staphylinus*. Reference may be made to the list of species given in Table 3 for, although the specimens were collected in the weed sampler, some of the species may have been planktonic.

Mites were occasionally taken in the plankton and two collected in June 1947 were identified as *Piona carnea* and *P. variabilis*.

Various species of wild duck visit the tarn occasionally and a heron (*Ardea cinerea*) sometimes comes to fish.

(*f*) *Comparison with other surveys*

Few comparable surveys appear to have been made. Laurie's (1942) description of a similar fishpond in Wales affords an interesting comparison, but it cannot be exact, since many of her insect nymphs and larvae are identified only to the genus.

A comprehensive survey of the continental literature has not been possible, but in the readily accessible journals nothing with which the present work can be compared has been discovered. At the beginning of the century complete fauna lists were in favour, and the work of Stenroos (1898) may be quoted as an example; but nothing strictly comparable with Three Dubs Tarn has been found and, in any case, the value of comparison with lists so old is open to question. Latterly the extensive continental work has concentrated on quantitative results and has not attempted to distinguish all the species encountered. One of the most detailed of all faunistic surveys is that of Berg (1938), but his work is primarily a transect from the shore to the middle of the lake along a few selected lines, and he did not study changes at different points around the lake in the shallow water.

4. POPULATION DENSITY

(*a*) *Mud fauna*

No quantitative work was done on the fauna of the bog, the surface, or the plankton, so there remains to be examined the results for the bottom mud and the weeds, and it is convenient to take them in that order.

The catches made with the Petersen Grab are set out in Table 7. The totals have been affected by the treatment with bone meal, and since, for the present, interest centres on the fauna of a typical tarn which has not been interfered with, all catches in Three Dubs Tarn after the first treatment must be disregarded. This leaves three hauls, one at station 12 in July 1936 and one at each station in March 1937. Some of the figures are very low, though not lower than in certain Swedish tarns which were of a similar type though not identical, one important difference being regular winter freezing with consequent depletion of oxygen over the mud (Lang, 1931). However, it was thought that the results from Three Dubs might have been due to inexperience with the technique and accordingly data from three similar nearby tarns, set out here in Table 11, were obtained. The amount of variation is unexpectedly small, the maximum number of animals per grab being 175 and the minimum being 103. There is no direct evidence

Table 8. *The commoner Diptera caught in cage S*

	Apr.	May				June				July					Aug.				Sept.				Oct.				Total	Total in cage *M*
	30	7	15	21	29	5	11	18	25	2	9	16	23	30	6	13	20	27	3	10	17	24	1	8	15			
CHIRONOMIDAE:																												
Tanypodinae																												
Pentaneura monilis (L.)	.	.	.	.	3	3	.	4	.	4	1	3	7	2	7	.	1	.	.	.	.	.	.	.	.		35	282
Procladius choreus (Mg.)	.	12	34	20	1	.	.	.	.	.	6	.	11	.	10	2	.	.	.	1	.	1	.	.	.		98	148
P. lugens Kieff.	.	.	17	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		32	37
P. flavifrons Edw.	.	.	.	.	.	.	5	11	4	2	11	.	6	2	5	.	.	.	.	.	.	.	.	.	.		46	33
Orthocladinae																												
Hydrobaenus (*Psectrocladius*) *platypus* Edw.	.	.	1	2	.	.	.	.	5	1	9	.	3	.	10	16	8	1	1	2	1	.	.	.	.		60	158
H. (*P.*) *limbatellus* Holmgr.	.	.	3	3	.	14	16	93	70	11	7	3	4	3	25	31	16	3	3	.	.	.	.	1	.		306	241
Corynoneura scutellata Winn.	.	.	.	.	.	.	.	.	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.		7	5
Chironominae																												
Pseudochironomus prasinatus (Staeg.)	.	.	.	.	.	.	.	.	.	.	2	4	5	3	2	.	.	.	.	.	.	.	.	.	.		16	0
Chironomus (*Chironomus*) *inermifrons* (Goet.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		0	187
C. (*C.*) *paganus* Mg.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		0	49
C. (*C.*) *pulsus* Walk.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		1	23
C. (*C.*) *nervosus* Staeg.	.	.	.	.	.	23	2	4	5	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		35	31
C. (*C.*) *lobiger* Kieff.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.		6	145
C. (*Microtendipes*) *pedellus* (Deg.)	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.		3	11
C. (*M.*) *chloris* var. *lugubris* Kieff.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		2	15
C. (*Polypedilum*) *prolixitarsis* Lundst.	.	.	.	1	1	.	.	.	1	14	12	4	1	.	.	.	.	.	.	.	.	.	.	.	.		34	1
C. (*Lauterborniella*) *orophilus* Edw.	.	.	.	.	3	8	4	3	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.		20	1
Tanytarsus gregarius Kieff.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		1	48
T. eminulus (Walk.)*	.	.	.	.	9	7	4	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		21	74
T. eminulus (Walk.)	.	.	.	.	.	.	.	.	.	.	3	2	3	5	6	5	.	1	1	2	2	.	.	.	.		30	105
T. nemorosus Edw.	.	.	.	.	.	.	.	10	18	9	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.		40	230
T. mancus (Walk.)	.	.	.	.	1	7	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		11	0
CERATOPOGONIDAE:																												
Bezzia solstitialis (Winn.)	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.		3	26
Probezzia venusta (Mg.)	.	.	.	.	.	.	.	.	1	1	.	2	1	2	.	.	.	.	.	.	.	.	.	.	.		7	10
Total, including species in Table 10	1	15	55	43	20	65	32	128	110	51	54	21	43	19	71	56	25	6	9	5	3	2	2	3	0	839	814	
Total, including unnamed species	1	?	?	63	83	139	81	239	329	?	128	65	99	51	83	250	92	51	25	11	7	7	2	5	1	1933	25†	
																											839	

* Originally identified as *T. holochlorus* Edw. † From Table 10.

Table 9. *The commoner Diptera caught in cage M*

	May					June				July					Aug.				Sept.				Oct.					Nov.				Total	Total in cage S
	30	7	15	21	29	5	11	18	25	2	9	16	23	30	6	13	20	27	3	10	17	24	1	8	15	22	29	4	11	17		
CHIRONOMIDAE:																																
Tanypodinae																																
Pentaneura monilis (L.)	.	.	.	1	80	10	26	26	16	18	36	28	7	11	9	7	1	2	2	1	.	1	.	.	.	.	.	.	.	.	282	35
Procladius choreus (Mg.)	.	10	52	15	1	.	.	1	2	.	13	7	3	11	5	6	12	2	1	.	2	2	3	.	.	.	.	.	.	.	148	98
P. lugens Kieff.	.	.	19	18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37	32
P. flavifrons Edw.	.	.	.	1	.	.	4	6	.	7	8	3	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	46
Orthocladiinae																																
Hydrobaenus (*Psectrocladius*) *platypus* Edw.	.	.	.	19	2	.	.	.	21	39	17	9	1	6	7	13	5	1	9	4	.	.	4	.	.	.	1	.	.	.	158	60
H. (*P.*) *limbatellus* Holmgr.	4	16	24	9	.	5	16	9	11	26	14	10	7	4	9	6	1	6	12	12	4	5	13	6	5	4	2	1	.	.	241	306
Corynoneura scutellata Winn.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	1	.	1	5	7
Chironominae																																
Pseudochironomus prasinatus (Staeg.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	16
Chironomus (*Chironomus*) *inermifrons* (Goet.)	.	.	.	.	.	.	.	.	.	.	.	5	21	29	34	22	47	26	2	.	1	.	.	.	.	.	.	.	.	.	187	0
C. (*C.*) *paganus* Mg.	.	.	.	.	.	.	.	.	.	.	.	6	3	3	8	24	5	.	.	.	.	.	.	.	.	.	.	.	.	.	49	0
C. (*C.*) *pulsus* Walk.	.	.	.	13	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23	1
C. (*C.*) *nervosus* Staeg.	.	.	.	3	18	2	7	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	31	35
C. (*C.*) *lobiger* Kieff.	.	.	.	52	24	.	1	.	.	.	.	.	.	19	49	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	145	6
C. (*Microtendipes*) *pedellus* (Deg.)	.	.	.	.	.	.	.	.	.	.	1	1	.	3	2	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	11	3
C. (*M.*) *chloris* var. *lugubris* Kieff.	2	5	3	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	2
C. (*Polypedilum*) *prolixitarsis* Lundst.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	34
C. (*Lauterborniella*) *orophilus* Edw.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	20
Tanytarsus gregarius Kieff.	.	.	.	11	20	.	.	.	.	.	.	.	1	.	.	1	.	9	1	4	1	.	.	.	.	.	.	.	.	.	48	1
T. eminulus (Walk.)*	.	.	.	.	5	12	40	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	74	21
T. eminulus (Walk.)	.	.	.	.	.	.	.	.	.	.	.	8	15	.	1	5	.	15	7	43	9	2	.	.	.	.	.	.	.	.	105	30
T. nemorosus Edw.	.	.	.	1	.	.	93	68	28	16	20	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	230	40
T. mancus (Walk.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0	11
CERATOPOGONIDAE:																																
Bezzia solstitialis (Winn.)	.	.	.	.	.	.	8	2	.	8	1	1	3	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26	3
Probezzia venusta (Mg.)	.	.	.	.	.	.	.	.	1	3	4	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	7
Total, including species in Table 10	6	40	100	148	162	31	197	133	81	119	115	83	64	90	127	89	74	64	37	71	17	10	23	7	5	4	3	2	0	1	1903	1860
Total, including unnamed specimens	7	42	101	149	267	98	222	163	110	154	128	116	113	146	313	240	199	149	103	72	29	14	34	11	6	4	3	2	0	1	2996	43† 1903

* Originally identified as *T. holochlorus* Edw.

† From Table 10.

Table 10. *The rarer Diptera caught in the floating cages*

		Total no. taken	No. of occasions	Total in cage *M*	Total in cage *S*	Dates
CHIRONOMIDAE:						
Tanypodinae	*Pentaneura melanops* (Mg.)	1	1	1	.	9 July
	P. barbitarsis (Zett.)	2	1	.	2	7 May
	P. cingulata (Walk.)	3	3	2	1	18, 25 June
	Anatopynia goetghebueri (Kieff.)	1	1	.	1	6 Aug.
	Procladius simplicistilus Freeman	4	2	4	.	7, 15 May
Orthocladiinae	*Metriocnemus marcidus* (Walk.)	4	2	.	4	13 Aug., 13 Sept.
	Cricotopus tricinctus (Mg.)	1	1	1	.	27 Aug.
	C. pulchripes Verr.	1	1	.	1	21 May
	Hydrobaenus (*Bryophaenocladius*) *apicalis* (Kieff.)	5	2	5	.	7 May, 10 Sept.
	H. (*B.*) *filiformis* Kieff.	1	1	.	1	29 May
	H. (*Limnophytes*) *minimus* (Mg.)	5	3	5	.	23 July, 3, 10 Sept.
	H. (*Smittia*) *pratorum* (Goet.)	3	2	3	.	7, 15 May
Chironominae	*Chironomus* (*Chironomus*) *macani* Freeman	3	3	3	.	18, 25 June, 2 July
	C. (*C.*) *camptolabis* (Kieff.)	3	3	2	1	30 July, 27 Aug., 3 Sept.
	C. (*Cryptochironomus*) *falcatus* Kieff.	5	2	5	.	10 Sept., 1 Oct.
	C. (*Endochironomus*) *tendens* (Fab.)	1	1	1	.	26 Aug.
	C. (*Polypedilum*) *convictus* Walk.	1	1	1	.	11 June
	C. (*Pentapedilum*) *flavipes* Mg.	2	2	1	1	3 Sept.
	C. (*P.*) *nubens* (Edw.)	1	1	1	.	11 June
	C. (*P.*) *uncinatus* (Goet.)	2	2	1	1	2 July, 1 Oct.
CULICIDAE:	*Chaoborus* (*Corethra*) *flavicans* (Mg.)	10	7	5	5	29 May, 5 June, 6, 13, 20 Aug.
CERATOPOGONIDAE:	*Palpomyia lineata* (Mg.)	1	1	1	.	18 June
	Bezzia annulipes (Mg.)	1	1	1	.	5 June
EPHYDRIDAE:	*Hydrellia griseola* Fallen	7	5	.	7	18 June, 2 July, 27 Aug., 24. Sept., 1 Oct.
	Total	68		43	25	

Table 11. *Collections with Petersen Grab in other tarns*

Tarn...	Wray	Mires	Fishponds		Scale Tarn		
Date...	1 22. ii. 41	1 22. ii. 41	2 22. ii. 41	3 10. iii. 41	9. xi. 37		
Station...	P	E			2	3	4
Chironomids	88	70	70	77	106	91	80
Ceratopogonids	1	1	.	.	1	2	1
Pisidium	3	21	71	.	7	1	1
Oligochaeta	.	.	.	.	1	.	1
Sialis	2	14	.	1	2	.	1
Hydracarina	3	3	17	29	6	3	24
Caenis	.	.	.	.	.	.	.
Leptocerus	.	.	.	.	.	.	.
Cyrnus	5	5	5	1	.	.	.
Phryganea	.	3	.	.	1	1	.
Triaenodes	.	.	.	.	.	.	.
Indet. Trichoptera	1	1	3	.	.	1	.
Chaoborus	.	.	3	.	.	.	1
Leptophlebia	9	10	4	12	.	.	.
Sympetrum	.	.	.	.	.	.	.
Coenagriids	.	.	2	.	.	.	.
Haliplus larva	.	.	.	.	.	.	.
Limnaea pereger	.	1	.	1	.	.	.
Hirudinea	1	.	.	.	.	.	.
Gammarus	.	.	.	.	.	3	1
Planorbis sp.	.	.	.	.	.	1	.
Total	113	129	175	121	124	103	110

of undue error in the original Three Dubs samples, but the safest course would seem to be to take the figures just quoted as typical of Lake District fishponds, although, perhaps, the lower limit is too high. The grab used covers an area of 750 sq.cm., so these figures must be multiplied by 13·3 to bring them to number per sq.m., and the answer is 2327 and 1370 respectively. These figures are unexpectedly high when compared with those quoted by Berg (1938), whose publication is, in effect, a review of the literature.

Bone meal was applied to the tarn at the rate of 10 cwt. to the acre to half the tarn in April 1937. No effect could be noted when samples were taken 3 months later, but in the following March the total fauna at station P, the station on the treated side, had increased to just over 1000 (Fig. 4). There was a small increase at the other station. In the spring after that the population of station P had fallen back, but that of station 12 showed a further increase. In 1939 the whole tarn was treated. Again no effect was seen until the following March. At neither station was the total as great as it had been at station P after the first

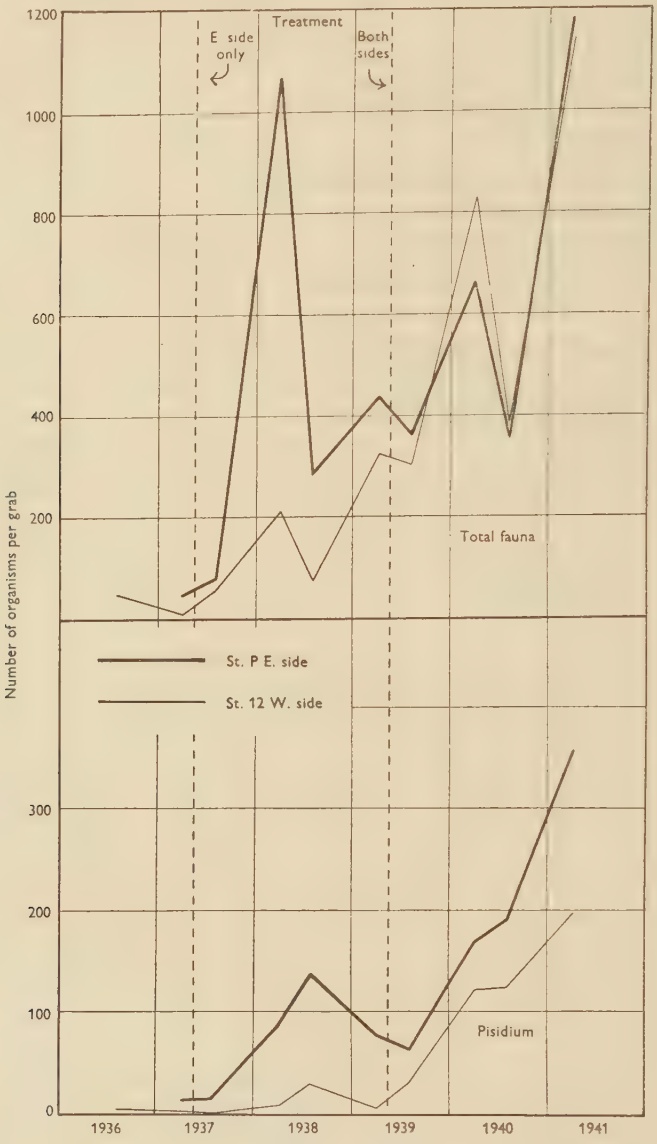

Fig. 4. The effect of bone meal on the bottom fauna of Three Dubs Tarn.

treatment, but this time the rise continued and in 1941 both stations had populations exceeding 1000. The total fauna is always less in July than in March, chiefly on account of the fewer chironomid larvae, but the numbers of *Pisidium*, shown in the lower graph of Fig. 4, are not subject to any seasonal fluctuation and show the trend more clearly.

Generalizations from such a small number of samples must be made with caution, but the figures from the two stations agree well, and it would seem that the effect of the bone meal has been to increase the bottom fauna about ten times. If a round figure of 1000 be taken as an approximation for the population per grab after treatment, the population per sq.m. is 13,300, which is remarkably high.

Berg (1938) examined the error in bottom-sampler technique and discusses the findings of other workers as well; he used a Birge-Ekman sampler which is probably a more efficient instrument than the Petersen Grab. He took ten samples close together at the same time, first in Esrom and then in Tjustrup Lake. The greatest deviation in a single sample from the mean population of the ten samples was 97·1 and 66·2 in the two lakes respectively.

How far the differences are due to errors in the technique and how far to variations in the density of the population in different parts of the mud must always be a difficult point to determine. It is interesting to examine the present samples from this aspect. There are ten samples from each station. In every sample there were more oligochaetes at station P than at station 12. The reverse holds good for mites, except in March 1937, when none was taken at either station, and July 1940 when the numbers were four at station P and two at station 12. Other animals distinctly more abundant at station P, though not preponderating there to the same extent as the oligochaetes, were *Cyrnus* and, in March only, ceratopogonids. The *Sialis* population at the two stations is very similar. These figures indicate a constant difference in the composition of the population of the two stations, and, since they lie but 30 m. apart and were found each time by the comparatively inaccurate means of cross-bearings, this conclusion was scarcely to be expected.

(*b*) *Weed fauna*

In July and August the total number of animals in 16 collections was 542, the lowest being 16, the highest 68, and the average 34; in March nine collections yielded 593 organisms, the lowest being 20 and the highest 241. The latter is so much higher than any other that it needs examining in detail. The sample was taken in a small tuft of *Apium* situated some 2–3 m. from the bank. As I waded across the intervening stretch of bare mud, I could see Corixidae fleeing before me and seeking refuge in the isolated patch of *Apium*. Possibly *Leptophlebia* did the same, and so the normal population of the area sampled was swollen by refugees. It seems reasonable to omit this one, and the total for eight stations is, therefore, 352 and the average 44. This higher average in March is mainly due to *Leptophlebia*, which has disappeared completely by summer. The numbers of other insects are less affected by the emergence of adults than might be expected. The small dragon-flies, *Pyrrhosoma* and *Enallagma*, have reached the end of their emergence period by July and yet the number of nymphs taken in that month is greater than in March. Probably they take more than one year to develop and some of them hide away in the mud like *Lestes*, *Sympetrum*, and *Aeshna* and therefore are not taken in the spring samples.

Seventeen samples off the delta yielded 522 specimens, and, if the exceptionally high sample of 20 March 1939 be omitted, seven samples in Boathouse Bay yielded 372 specimens. The mean of these 24 samples is 37. The catch at six out of the seven stations in Boathouse Bay exceeds this mean, and the differences are found to be significant by the binomial test. Boathouse Bay is sheltered from the prevailing wind, and in summer it is still further protected by the bed of *Equisetum* which grows across its mouth. It also receives inflow 1 which has a higher calcium concentration than any of the other inflowing streams, and either of these factors might be the cause of the denser population. This was the only statistical correlation found. Annual fluctuations, and differences between different species of plant were doubtless not apparent because the number of samples was not large enough.

The collections off the delta are probably more typical of the whole tarn than those in Boathouse Bay. If all the stations from off the delta are included, the range is 16–68 organisms per haul with a mean of 30 and a standard deviation of 15.

The hand-grab originally used was 1 ft. or 30·48 cm. square; the final model, built after the war, covered one tenth of a square metre and so had sides 31·6 cm. long. But, since any answer is bound to be rough, the error introduced by multiplying all the figures by ten to give number per square metre may be ignored.

The population per square metre is, therefore, of the order of 300 weed-dwelling organisms excluding chironomid larvae, and the range will be from 150 to 450 if the standard deviation be taken as a guide. This is a small population. Reference may be made to a discussion of number of animals per unit area in rivers given by Pentelow, Butcher & Grindley (1938).

5. PHYTOPLANKTON

Collections of phytoplankton were made from April 1947 to June 1948, roughly once a week, by means of a small tow-net hauled down the length of the tarn.

Table 12. *Summarized records of the rarer algae of the phytoplankton*

			No. of times recorded	Months in which recorded
Chlorophyceae	Volvocales	*Gonium sociale* (Duj.) Warming	2	iv
		Tetraspora lacustris Lemm.	5	viii, x, xi
		Stylosphaeridium stipitatum Geitler	5	i, ii, v, xi, xii
	Chlorococcales	*Ankistrodesmus falcatus* (Corda) Ralfs.	9	i, iv, vi, ix, xi
		var. *acicularis* (A.Br.) G. S. West	1	i
		var. *duplex* (Kütz.) G. S. West	6	vi, vii, ix
		var. *mirabilis* W. & G. S. West	1	iii
		Pediastrum boryanum (Turp.) Menegh.	4	i, ii, ix, xi
		Crucigenia irregularis Wille	1	ix
		Scenedesmus dimorphus (Turp.) Kütz.	1	xi
		S. bijuga (Turp.) Lagerh.	1	i
	Conjugales	*Spirotaenia condensata* Bréb.	14	i, iii, iv, v, vi, ix, xi
		Closterium jenneri Ralfs.	1	iv
		C. kützingii Bréb.	12	i, ii, iii, iv, v, vi, vii, ix, xi
		Euastrum oblongum (Grev.) Ralfs.	4	i, v, xi
		E. ansatum Ralfs.	3	i, iii
		E. bidentatum Näg.	4	i, iv, vi
		E. verrucosum Ehrenb.	5	i, ii, iv, ix, xi
		Micrasterias truncata (Corda) Bréb.	3	v, ix
		M. papillifera Bréb.	4	iv, v, vi
		M. apiculata (Ehrenb.) Menegh.	10	i, viii, ix, x, xi
		M. rotata (Grev.) Ralfs.	6	i, iv, vi, ix, xi
		M. denticulata Bréb.	2	iv
		Cosmarium subtumidum Nordst.	9	i, ii, iii, iv, v
		C. ? margaritatum (Lund.) Roy & Biss.	7	ix, x, xi, xii
		Xanthidium antilopaeum (Bréb.) Kütz.	1	i
		X. cristatum var. *uncinatum* Bréb.	1	i
		Arthrodesmus incus (Bréb.) Hass.	4	iii, iv, vi
		var. *ralfsii* W. & G. S. West	3	iii, v
		A. triangularis Lagerh.	5	iv, v, vi
		var. *subtriangularis* (Borge) W. & G. S. West	1	vii
		A. octocornis Ehrenb.	4	i, vii
		Staurastrum brevispinum Bréb.	10	i, vi, vii, viii, x, xi, xii
		S. glabrum (Ehrenb.) Ralfs.	4	i, ii, xi, xii
		S. dickiei Ralfs.		
		var. *rhomboideum* W. & G. S. West	1	iv
		S. connatum (Lund.) Roy & Bliss.	2	i
		S. curvatum West.	1	xi
		S. lunatum Ralfs.	3	i, v
		S. brasiliense var. *lundellii* W. & G. S. West	5	viii, ix, xi
		S. polytrichum (Perty) Rabenh.	1	xi
		S. teliferum Ralfs.	4	i, vi, xi
		S. paradoxum Menegh.	2	vii,
		S. anatinum Cooke and Wills.	3	iv, vi
		S. aculeatum (Ehrenb.) Menegh.	4	i, v, xi
		S. furcigerum Bréb.	1	ix
		Cosmocladium constrictum Arch.	14	i, v, vi, vii, viii, x, xi
		Spondylosium planum (Wolle) W. & G. S. West	3	iv, ix
		Hyalotheca dissiliens (Sm.) Bréb.	9	i, ii, iii, iv, v, vi
		Desmidium swartzii Ag.	4	iv, v, vi, ix
		Closterium libellula Focke	1	iv
	Chaetophorales	*Microthamnion kützingianum* Naeg.	1	v

Table 12. (*cont.*)

			No. of times recorded	Months in which recorded
Chrysophyceae	Chrysomonadales	*Chrysococcus rufescens* Klebs	1	vii
Bacillariophyceae		*Tabellaria flocculosa* (Roth) Kütz.	8	ii, iii, iv, vi
		T. fenestrata (Lyngb.) Kütz.	6	i, iv, vii, ix, xi
Dinophyceae	Dinoflagellata	*Gymnodinium aeruginosum* Stein	2	i, iv
		G. fuscum (Ehrenb.) Stein	16	i, ii, iii, iv, v, vi, ix, x, xi
Euglenineae		*Phacus longicauda* (Ehrenb.) Duj.	2	vi, ix
		Trachelomonas varians Defl.	2	vi, xi
		forma *minor* Lund	1	ix
Myxophyceae	Chroococcales	*Merismopedia glauca* (Ehrenb.) Naeg.	2	ii
		M. tenuissima Lemm.	1	ix
	Hormogoneales	*Anabaena flos-aquae* (Lyngb.) Bréb.	3	vi
	inc. sed.	*Gloeochaete wittrockiana* Lagerh.	1	xi

Dr Lund has expressed the frequency of the various species in the catch in the conventional botanical adjectives: abundant (a.), frequent (f.), occasional (o.), rare (r.), and very rare (v.r.), with sometimes one or more plus signs after an 'a.' to indicate an unusually great population. These values have been used to construct Fig. 5 which includes only the commoner species, that is those which for a period, possibly short, were an important constituent of the population, and those which, though never abundant, were recorded on many occasions. Table 12 shows the rarer species, that is those which were taken neither abundantly nor often, the data being presented in a more condensed form. There are 25 species and varieties in Fig. 5, 63 in Table 12, and in addition there were 47 rare species to which it was not possible to put a specific name. There were, therefore, 136 species and varieties recorded from the plankton in the course of just over one year.

A striking feature is the rate at which the composition of the population changes. *Eudorina elegans* was found on every occasion, *Botryococcus braunii* on all but one, and *Mallomonas caudata* was fairly consistently present. But all the other species which at one time or another were abundant were apparently absent from the plankton for long periods. Altogether, 14 species attained 'abundance', but of these no less than six were never recorded as abundant in two consecutive catches. *Botryococcus braunii* was abundant for some 4 months, all through the winter, a stretch unequalled by any other species. Two others were abundant continuously for about 2 months, *Eudorina elegans* in spring and *Characium gracilipes* in summer. It is evident from these results that any attempt to classify water-bodies of this type on the phytoplankton must be based on frequent observation extending throughout a year.

The long list of desmids (Conjugales) is characteristic of waters of this type, but certain species in other groups, notably *Eudorina elegans*, *Volvox aureus*, *Gonium pectorale*, and *Colacium arbuscula* are more typical of richer lowland pools and scarcely to be expected in Three Dubs Tarn. Possibly their presence is attributable to the bone meal.

Characium gracilipes is primarily an epiphyte on the Cladoceran, *Diaphanosoma brachyurum*, and its occurrence as a true plankton form was unexpected.

Dr Marie Rosenberg examined the phytoplankton in July and September 1936 and in March 1937, that is on three occasions before the tarn had received any treatment. In July she records 17 species belonging to nine genera. Unfortunately, few specific names are given, but all the genera were found again in the tarn in 1947. Of these 17 all but *Tabellaria fenestrata* are desmids (Conjugales). In September the picture has not changed greatly, though species names are now given and it is seen that there are some which have not been recorded since. In March 1937 *Hyalobryon* sp. is abundant, and this is a genus which was not found in later years, but nearly all the other names are familiar. *Dinobryon cylindricum* is frequent, and, as this is quite likely to be a misidentification of *D. sertularia*, since Lund confused the two for over a year, the list, with certain exceptions about to be discussed, is similar to that of March 1948.

The tarn was treated for the first time in April 1937, and Rosenberg examined the phytoplankton in August. *Anabaena lemmermanii* was the commonest organism on 7 August, but by 20 August it had given place to *Uroglenopsis americana* and an unspecified *Dinobryon*. Neither of these two species has been recorded in later years. Mentioned for the first time in January 1938, when it was abundant under thin ice, *Volvox aureus* appears in all the subsequent lists. In April 1938 *Dinobryon sertularia* is the most abundant species, and other common species of the 1947/8 lists appearing for the first time are *Botryococcus braunii*, *Eudorina elegans*, *Volvox aureus* and *Gonium pectorale*. *Mallomonas mirabilis*, first recorded in 1937, may be *M. caudata*. In March and

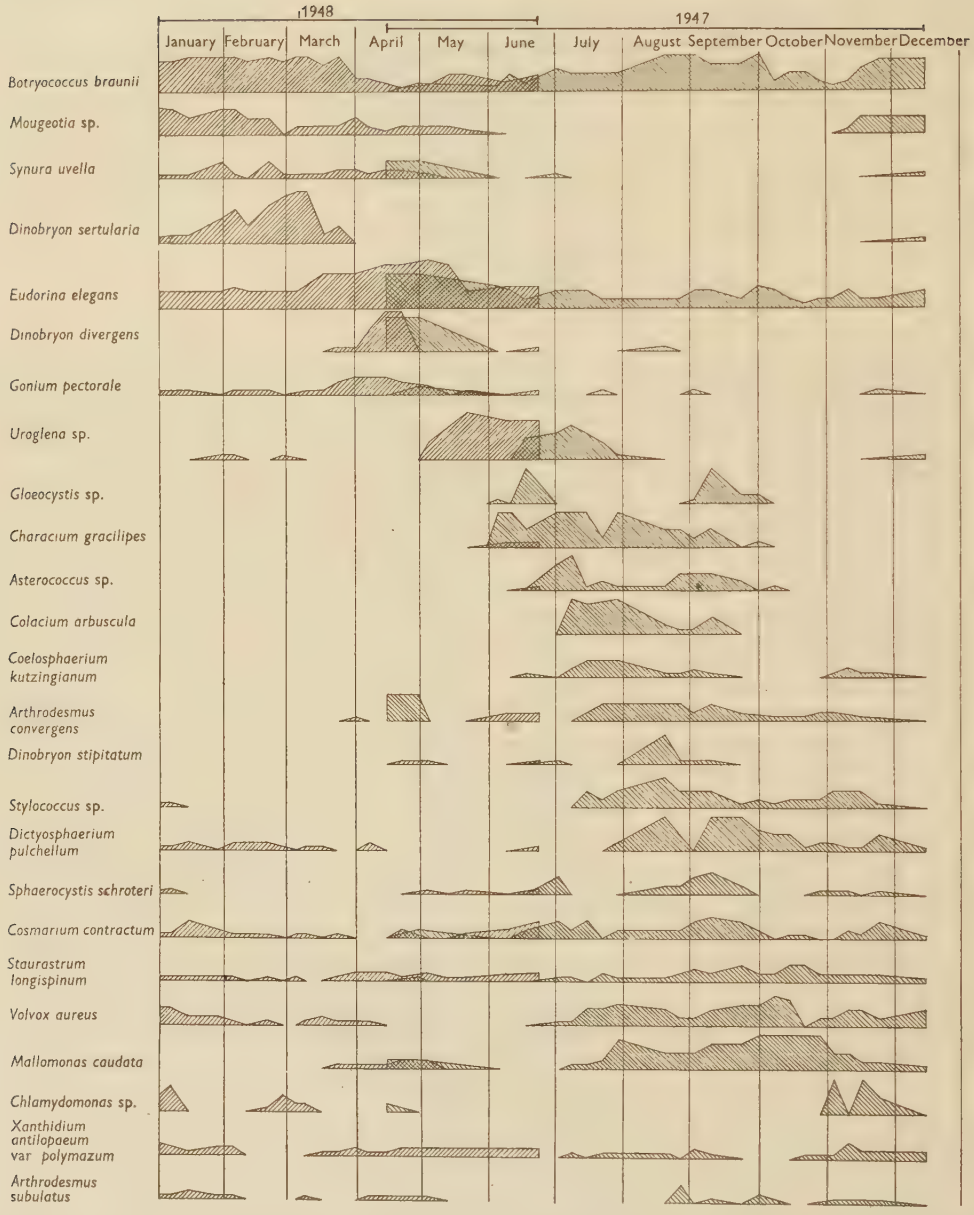

Fig. 5. The occurrence of the commoner members of the phytoplankton in Three Dubs Tarn. Observations extended from April 1947 to June 1948, but the diagram begins at January and the two years are distinguished by hatching of different slope. The results have been plotted according to the following scheme: v.r.=2, r.=4, r.—o.=6, o.=8, o.—f.=10, f.=12, f.—a.=14, a.=16, a.+=18, and a.++=20 points on the vertical scale.

August 1938 the population was much as it had been a year previously. These results bear out the belief that the presence of certain species is related to the treatment of the tarn with bone meal.

The occurrence of the commoner species is shown in Fig. 5. The year is started with January and both sets of data for the months which overlapped are included. On the whole the picture is similar in the two years; *Eudorina elegans* and *Dinobryon divergens* had a period of abundance in April in both years, but *Uroglena* sp. was more predominant in 1948, and *Characium gracilipes*, abundant in June 1947, had only just appeared in June 1948. The number of rarer species common to both years was seven out of a total of ten in April and five out of seven in June. Comparison with the more fragmentary results for earlier years confirms the impression that the annual sequence is similar but not identical.

6. THE EFFECT OF BONE MEAL

This subject has already been discussed under each appropriate head, but it seems useful to gather all the information together in one section. That statistical analysis shows no increase in the fauna of the vegetation may be due to inadequate sampling, but if there has been any increase it has been quite small. There are no quantitative data for the plankton, but certain qualitative changes in the phytoplankton are probably due to the bone meal.

The biggest change has been in the deeper water. The number of animals living in the mud has increased and, though only cautious statements can be based on the number of samples taken, the increase appears to be about tenfold.

Most of the deeper parts of the tarn were originally bare, but now support a thick growth of *Nitella*, and the spread of this plant has enabled certain of the weed-dwellers, notably the small dragon-fly nymphs, and, to a less extent, some of the Trichoptera, to extend their range from the shallow water. Others have remained confined to the shallow water, the outstanding examples being *Corixa* and *Leptophlebia*, the two most abundant groups inhabiting vegetation. *Cloëon* is now more abundant than it was originally, but whether the bone meal has affected it through the vegetation or more directly is impossible to say.

It is not possible to reach comprehensive conclusions about the effect on individual species, but the population of Corixidae and Gastropoda is still that typical of a base-deficient moorland tarn.

7. ANIMALS AVAILABLE FOR FISH TO EAT

The fish and their food is to be the subject of a separate paper, but it is relevant to the present study to point out what animals are most available at different seasons. The food actually found in the fish stomachs should make interesting comparison with this information.

In January and February there is little in the plankton for the fish to eat, and it may be predicted that their food comes from the bottom and from the weeds. Chironomids, *Pisidium*, *Leptophlebia*, and corixids are the most abundant animals. For a short period in March and again in April tadpoles are available as the eggs first of frogs and then of toads hatch. In April, planktonic animals begin to increase, and from this month onwards the fish may also find the pupae of chironomids.

In May, chironomid pupae are very numerous, and possibly *Leptophlebia* is more readily available as it also is travelling to the surface to emerge. These animals will also be available in the adult stage on the surface.

By July, *Leptophlebia* will be over, but *Caenis* is just emerging and its nymphs may be expected in fish stomachs, possibly for the first time, since in other months they are concealed in the mud and probably difficult to find. That the adults are eaten is well known, for they have a special fisherman's name, White Midge or Angler's Curse.

In the autumn months food is probably harder to find than at any other time of the year. A fair amount is to be obtained at the surface, much of it terrestrial animals, which have arrived at the surface by accident. In the bottom mud, *Pisidium* is abundant, though chironomids are much reduced in numbers. Among the weeds, corixids and their nymphs are the most numerous animals and dragon-flies are fairly common, some of the larger ones being found in the weeds at this time. The small Odonata nymphs are fairly abundant all through the year and some of the Trichoptera larvae are also present at all seasons, though their numbers are not as great as those of the other animals mentioned.

8. COMPARISON OF POND-NET AND HAND-GRAB

On a certain number of occasions, as has already been mentioned, collections were made both with a hand-grab and with a pond-net. The net collecting was not done in a systematic way. No attempt was made to cover a standard area, nor was the catch sorted with the care devoted to grab samples. It was believed that the net covered a much wider area and would consequently catch scarce species so few and far between that the grab might be expected to miss them. An analysis of the results to discover whether the net did fulfil this purpose would appear to be of interest.

The first part of Table 13 shows the number of times certain of the less common animals were caught. An average shows that the net did have a very slight tendency to collect the rarer things more often than

the grab, but the difference is too small to be of any practical account. Of the species included in Table 13 two, *Cloëon* and *Notonecta*, were taken by the net but not by the grab, but for two others, *Gammarus* and *Deronectes 12-pustulatus*, the reverse is true. So the use of the pond-net did not achieve its object and, had the grab only been used, no serious error in the picture of the fauna would have resulted. The second part of Table 13 shows the total numbers caught by the two methods. It is probably significant that active swimmers, such as the corixids and *Leptophlebia*, which seek to escape from a strange object by flight were captured in greater numbers by the net than by the grab; whereas inactive animals, such as the Trichoptera, which probably rely on the cover provided by vegetation for safety did not preponderate in the net catches. A pond-net, therefore, is evidently a selective instrument.

Table 13. *Comparison of two methods of collecting*

	Spring collections 1937–40		Summer collections 1936–40	
	Hand-grab	Pond-net	Hand-grab	Pond-net
(*a*) Number of times certain scarce animals were caught				
No. of stations...	9	11	11	9
Hirudinea	2	2	4	2
Limnaea pereger	1	3	2	0
Gammarus	1	0	2	0
Cloëon	0	3	0	0
Nemoura	2	3	0	0
Sympetrum	0	0	5	5
Aeshna	0	0	2	2
Deronectes 12-pustulatus	1	0	0	0
D. depressus	1	0	1	1
Haliplus fulvus	2	1	4	4
H. ruficollis	0	1	0	0
Notonecta	0	0	0	1
Dipterous larvae	2	1	0	0
Newts and newt-tadpoles	0	1	4	5
Total	12	15	24	20
Average	1·33	1·36	2·18	2·22
(*b*) Total numbers caught				
Hirudinea	3	3	9	2
Limnaea pereger	1	9	7	0
Hydracarina	20	7	22	44
Gammarus	18	0	3	0
Leptophlebia	242	710	0	0
Cloëon	0	5	0	0
Nemoura	6	6	0	0
Coenagriidae	29	133	51	201
Aeshnidae and Libellulidae	0	0	10	31
Corixidae	203	1235	183	424
Coleoptera	4	3	7	13
Trichoptera	65	71	41	38
Dipterous larvae	2	1	0	0
Newts and newt-tadpoles	0	1	7	20

9. ACKNOWLEDGEMENTS

Reference to the kindness of Mr Illingworth, who placed facilities for the work at our disposal, has already been made. It will have been evident from the text that I am under a deep debt of gratitude to my colleagues of the Freshwater Biological Association. Dr J. W. G. Lund has named the higher plants and provided all the data on which the account of the phytoplankton is based; Dr C. H. Mortimer and Mr F. J. Mackereth have between them carried out all the water examination; and Miss C. Kipling has assisted with the statistical analysis. Mr S. J. Mitchell constructed the hand-grab and was responsible for the design of most of the detail. I also acknowledge gratefully the assistance of Mr K. Shepherd.

The work of putting reliable specific names to the plants and animals taken would have been impossible

had not a number of experts consented to do it, and I wish to put on record my sincere thanks to Mr G. O. Allen (*Nitella*), Dr T. B. Reynoldson (Platyhelminthes), Mr S. Prudhoe, assistant to Dr H. A. Baylis (Oligochaetes), Mr C. Oldham (*Pisidium*), Dr Karl Viets and Mr William Williamson (Hydracarina), Mr D. J. Scourfield, I.S.O. (Crustacea), Dr H. B. N. Hynes (Plecoptera), Mr D. E. Kimmins (Trichoptera), Prof. F. Balfour-Browne and Rev. E. J. Pearce (Coleoptera), Mr P. Freeman (Chironomidae), Mr H. Oldroyd (Ephydridae), and Mr R. Coe (Tipulidae).

I wish to thank also Mr John Clegg who took the photographs and provided the prints from which the plates have been made.

10. SUMMARY

1. Three Dubs Tarn (Pl. 7) is an artificial tarn about 10 ft. deep, 4 acres in extent, and 700 ft. above sea-level. It is a moorland fishpond, typical but for the fact that bone meal is added to it every second year.

2. The water is clear, poor in electrolytes, and high in dissolved organic matter. The calcium concentration ranged from 3·0 mg./l. during a wet spell in winter to 5·2 mg./l. during a fine spell in summer. The effect of the bone meal on the calcium concentration was probably transient.

3. A tow-net for plankton and a Petersen Grab for mud fauna were of standard type. A special grab was devised for sampling the fauna of the weeds, and emerging insect adults were caught in a floating cage.

4. The vegetation was mapped in 1936 and 1947. In 1936 most of the bottom of the tarn in deeper water was bare, in 1947 it was covered with *Nitella*, and this plant may have developed as a result of the bone-meal treatment. Other changes are discussed, and some are thought to be due to the fact that the later survey was based on a more careful examination.

5. The surface fauna consists only of *Gerris lacustris* and *G. odontogaster* which are not very numerous in bays, and *Microvelia reticulata* in the emergent vegetation.

6. In the weeds *Corixidae* and *Leptophlebia* (Ephemeroptera) are the most abundant animals; *Gammarus* and Mollusca are notably scarce, *Limnaea pereger* being the only species of the latter. *Leptophlebia* emerges during early summer and nymphs are absent in July. The species of insect have been discovered partly by breeding out, but mainly from the catches in the floating cages. These give also a picture of the emergence periods.

7. A small area at one side of the tarn was overgrown with *Sphagnum* and other vegetation. The fauna was an attenuated version of that of the rest of the tarn with some notable additions such as *Limnaea glabra*, tipulid larvae, Platyhelminthes, and a number of Coleoptera.

8. Collections were made with a Petersen Grab. It is a typical soft-water mud fauna augmented by certain weed-dwellers whenever the grab struck a patch of *Nitella*. But some of the commonest weed-dwellers, notably *Leptophlebia* and Corixidae, did not extend into deeper water. The specific identity of the insect mud-dwellers was obtained from the floating cages. The cages were emptied once a week and therefore give information about emergence periods.

9. No regular zooplankton collections were made, and it is not possible to do more than give lists and notes on abundance on a few isolated dates. Fish are to be considered in a separate paper.

10. The bottom mud of three nearby similar tarns had 1000–2000 organisms per square metre. The hauls in Three Dubs before treatment with bone meal yielded less than this, but some error due to inexperience is possible. This population is unexpectedly large compared with what has been found elsewhere.

11. As a result of the treatment with bone meal the mud fauna seems to have increased about tenfold.

12. Excluding chironomids, since weed dwellers cannot be distinguished from mud-dwellers, some 300 animals inhabit 1 sq.m. of vegetation. This is a low population when compared with other records.

13. Twenty-five species of algae occurred abundantly in the plankton for a period which might be quite short, or, without ever attaining abundance, were present over a long period. About five times as many species were never abundant, and were taken on a few occasions only. The rate at which the population changed from week to week was one of its most striking features. There is evidence that several species have come in since the bone-meal treatment started and are not typical of such a place.

14. Comparison of the catches made with the hand-grab and the pond-net suggest that the pond-net is a selective instrument. The belief that it is likely to catch rare species so few and far between as to be missed by the grab is unfounded.

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THE DISTRIBUTION OF WILD DEER IN SCOTLAND

By WILLIAM LING TAYLOR

(With one Map)

Following the compilation of lists of the deer populations in the Forestry Commission's areas in England and Wales in 1938 and again in 1948 (Taylor, 1939, 1948), a number of requests have been made for similar information concerning the State afforestations in Scotland. Accordingly, a survey has this year (1949) been made by the Commission's Foresters locally in charge of the forests referred to in the appended list with the co-operation of Sir Henry Beresford-Peirse, the Commissioners' Director for Scotland, and the Conservators of Forests and Forest Officers concerned. I am indebted to the technical staff of all grades in Scotland, without whose willing help and interest the list now available could not have been prepared. While in no way intended to represent a record of the present distribution of the various species of deer to be found running wild in Scotland, the list gives an indication of the widespread areas over which the native red and roe deer occur, and of localities in which fallow deer and the exotic Japanese species are present. The small number of State forests to the south of the Highland Line in which no deer have been observed are omitted from the list.

As would be expected the usual habitat of the red deer (*Cervus elaphus*) lies over the extensive mountain and moorland areas of the north and west where the species is often to be found in large numbers. Extensive herds of red deer are also present in parts of Aberdeenshire and in central Scotland, and again in one or two stations in the south, but in reading the survey in regard to red deer it must be borne in mind that the boundaries of some of the Commission's Highland and other forests in Scotland are deer-fenced, and, although red deer may not be numerous within these fences, they frequently occur in large congregations over the open terrain round about. Deer fencing (6½ ft.) has proved a satisfactory although, as might be expected, not a complete deterrent. It is, of course, impossible to tolerate red deer in any but the smallest of numbers on newly afforested ground, and among young growing plantations.

If the industralized areas are excepted, roe deer (*Capreolus capreolus*) can be regarded almost as ubiquitous throughout the mainland of Scotland. The degree of stocking varies widely with local circumstances but, where covert exists, their numbers are frequently considerable. Roe deer populations tend to increase in almost all localities where extensive afforestations are carried out and, in excesssive numbers, roe can also be very destructive to young plantations, both by browsing and by the use of young saplings as fraying stocks by the bucks in due season. In these circumstances it is obligatory to take measures to regulate local stockings, but it is safe to say that, given adequate covert in sufficient area, the extermination of this graceful little native deer is, in practice, a matter of impossibility if only on the ground of expense, and consequently it is nowhere attempted. Except where red deer are also present in the neighbourhood it is not the custom of the Commission to deer-fence their forests, consequently the roe have easy access to many areas, a fact that not infrequently leads to difficulties sooner or later because the roe is a rapid breeder, twin births being not at all uncommon.

So far as the Forestry Commission's Scottish areas are concerned the only acclimatized species is the Japanese deer (*Sika nippon*). This deer occurs as far north as Loch Shin and, in small numbers, at two stations in Ross and Cromarty and two in Inverness-shire; it also occurs in somewhat greater numbers in the Mull of Kintyre and again 'occasionally' on the borders of Fife and Clackmannanshire.

Fallow deer (*Dama dama*) are present at several widely distributed stations but, with the exception of the Drummond Hill district of Perthshire, are nowhere reported to be strong in numbers.

None of the further species which have become acclimatized in parts of England such as the Siberian roe (*Capreolus pygargus*) and the Chinese muntjac (*Muntiacus reevesi*) have been observed in or about the State forests in Scotland and no exotic species are reported other than Japanese deer (*Sika nippon*).

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SCOTLAND
1 CAITHNESS
2
3
4
5 SUTHERLAND
6
7
8
9
10
11
12
13
14
ROSS and CROMARTY
15–18
19
20 NAIRN
21–22
23
24
25
26–34
INVERNESS
35
36
37
38
SKYE
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44 MORAY
45–47
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BANFF
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ABERDEEN
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78 KINCARDINE
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ANGUS 82
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PERTH
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73–4
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MULL
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92–94
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ARRAN
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FIFE
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112
113
114
CLACKMANNAN
KINROSS
DUMBARTON
STIRLING
WEST LOTHIAN
EAST LOTHIAN
MIDLOTHIAN
RENFREW
LANARK
115
116
117
PEEBLES
SELKIRK
118 BERWICK
ROXBURGH
119
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131
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133
134
135
137–8
DUMFRIES
KIRKCUDBRIGHT
WIGTOWN
136
NORTHUMBERLAND
CUMBERLAND
ENGLAND

Table 1.

County	Forest No.	Forest Name	Species	Density
Caithness	1	Rumster	None observed	
Sutherland	2	Borgie	Red	Not numerous
			Roe	,, ,,
	3	Dornoch	Red	Occasional
			Roe	Not numerous
	4	Balblair	,,	Numerous
	5	Shinn	Red	Not numerous
			Roe	,, ,,
			Japanese	Occasional
Ross and Cromarty	6	Lael	Red	Numerous
			Roe	,,
	7	Slatterdale	Red	Not numerous
			Roe	,, ,,
	8	Achnashellach	Red	,, ,,
			Roe	,, ,,
			Japanese	Occasional
			Fallow	,,
	9	Strome N. & S.	Red	Not numerous
			Roe	,, ,,
	10	Inverinate, Ratagan, Glenshiel	Red	,, ,,
			Roe	,, ,,
	11	Longart	Red	Occasional
			Roe	Not numerous
			Japanese	Occasional
			Fallow	,,
	12	Strathconon	Red	Not numerous
			Roe	Occasional
	13	Ardross	Red	,,
			Roe	Not numerous
	14	Morangie	Red	Occasional
			Roe	Not numerous
	15	Findon	,,	Numerous
	16	Kessock	,,	Occasional
	17	Kilcoy	,,	Not numerous
	18	Milbuie	,,	,, ,,
Inverness-shire	19	Craig Phadrig	Roe	Not numerous
	20	Culloden	,,	,, ,,
	21	Strathdearn	,,	Occasional
	22	Strathnairn	Red	Numerous
			Roe	Occasional
	23	Farigaig	Red	,,
			Roe	Not numerous
			Japanese	,, ,,
	24	Glenurquhart	Red	Occasional
			Roe	Numerous
	25	Guisachan	Red	,,
			Roe	,,
	26	Craignaneum	Red	Not numerous
			Roe	Numerous
			Japanese	Occasional
			Fallow	,,
	27	Inchriach	Roe	Not numerous
	29	Queen's (Glen More)	Red	Numerous
			Roe	,,
	29	Port Clair	Red	Not numerous
			Roe	Numerous

Table 1 (*cont.*)

County	Forest No.	Forest Name	Species	Density
Inverness-shire (*cont.*)	30	Inchnacardoch	Red	Numerous
			Roe	,,
	31	Glengarry and South Laggan	Red	,,
			Roe	Not numerous
	32	Leanachan	Red	,, ,,
			Roe	,, ,,
	33	Glen Loy	Red	,, ,,
			Roe	,, ,,
	34	Nevis	Red	Numerous
			Roe	,,
	35	Glenrigh	Red	Not numerous
			Roe	,, ,,
(Skye)	36	Glenbrittle	Red	,, ,,
	37	Eilanriach	,,	,, ,,
			Roe	Occasional
	38	Clunes	Red	Not numerous
			Roe	Numerous
Nairnshire	39	Assich	Roe	Not numerous
	40	Ferness	,,	Numerous
Moray	41	Culbin	Roe	Numerous
	42	Roseisle	,,	Not numerous
	43	Lossie	,,	Numerous
	44	Newtyle	,,	Not numerous
	45	Dallas	,,	,, ,,
	46	Newton (nursery)	,,	Occasional
	47	Monaughty	,,	,,
	48	Teindland	,,	,,
	49	Speymouth	,,	Numerous
			Red	Occasional
	50	Scootmore	,,	,,
			Roe	Numerous
Banffshire	51	Rosarie	Roe	Occasional
Aberdeenshire	52	Deer	Roe	Numerous
	53	The Bin	,,	Not numerous
	54	Clashindarroch	,,	,, ,,
			Red	Occasional
	55	Auchernach	,,	,,
			Roe	Not numerous
	56	Whitehaugh	,,	,, ,,
			Red	Occasional
	57	Tilliefoure	,,	,,
			Roe	Not numerous
	58	Pitfichie	,,	Numerous
	59	Kemnay	,,	Not numerous
	60	Kirkhill	,,	Numerous
	61	Countesswells	,,	Not numerous
	62	Midmar	,,	,, ,,
	63	Alltcailleach	Red	Numerous
			Roe	,,
	64	Corrennie	,,	Not numerous
Perthshire	65	Rannoch	Red	Numerous
			Roe	,,
	66	Allean	,,	,,
			Red	Occasional
	67	Drummond Hill	,,	Not numerous*
			Roe	Numerous
			Fallow	Not numerous*

* Numerous in district

Table 1 (*cont.*)

County	Forest No.	Forest Name	Species	Density
	68	Craigvinean	Red	Not numerous
			Roe	,, ,,
			Fallow	,, ,,
	69	Blackcraig	Red	Occasional
			Roe	Numerous
	70	Strathord	,,	,,
	71	Kinfauns	,,	Occasional
	72	Keillour	Red	,,
			Roe	Not numerous
	73	Strathyre	Red	,, ,,
			Roe	,, ,,
	74	(Tulloch)	,,	,, ,,
			Red	Numerous
	75	Loch Katrine	,,	Occasional
			Roe	,,
			,,	Numerous
	76	Loch Ard	Red	,,
Kincardineshire	77	Blackhall	Roe	Not numerous
	78	Durris	,,	,, ,,
			Red	Occasional
	79	Fetteresso	,,	,,
			Roe	Not numerous
	80	Drumtochty	,,	Numerous
	81	Inglismaldie	,,	,,
Argyllshire	83	Glenhurich	Red	Numerous
			Roe	Not numerous
(Mull)	84	Salen	Red	,, ,,
	85	Fiunary	,,	Numerous
			Roe	Not numerous
	86	Duror	Red	,, ,,
			Roe	,, ,,
	87	Barcaldine	Red	Occasional
			Roe	Numerous
	88	Fearnoch	,,	,,
			Red	Occasional
	89	Inverinan	,,	Not numerous
			Roe	Numerous
	90	Inverliever	,,	Not numerous
			Red	Occasional
	91	Eredine	,,	Numerous
			Roe	Not numerous
	92	Kilmichael	Red	Numerous
			Roe	Occasional
	93	Minard	,,	Not numerous
			Red	,, ,,
	94	Asknish	,,	Occasional
			Roe	Not numerous
	95	Knapdale	Red	Occasional
			Roe	Numerous
	96	Achaglachgach	,,	,,
			Red	,,
			Japanese	Occasional
	97	Carradale	,,	Numerous
			Fallow	Not numerous
			Roe	Occasional*
	98	Saddell	Japanese	Numerous
			Roe	Occasional

* Roe reported to be increasing

Table 1 (*cont.*)

County	Forest No.	Forest Name	Species	Density
Argyllshire (Mull) (*cont.*)	99	Strathlachan	Roe	Occasional
	100	Glendaruel	,,	,,
			Red	,,
	101	Glenbranter	,,	Not numerous*
			Roe	Numerous
	102	Glenfinart	Red	Occasional
			Roe	Not numerous
	103	Ardgartan	Red	Occasional
			Roe	,,
	104	Benmore	Red	Not numerous
			Roe	Numerous
	105	Corlarach	,,	Not numerous
Angus	106	Glenisla	Red	Numerous
	82	Montreathmont	Roe	Occasional
Fife	107	Tentsmuir	Roe	Not numerous
	108	Edensmuir	,,	,, ,,
	109	Carden	,,	Occasional
	110	Blairadam	,,	,,
Fife and Clackmannanshire	111	Devilla	Roe	Occasional
			Japanese	,,
	112	Tulliallan	Roe	,,
Stirlingshire	113	Garadhban	Roe	Occasional
	114	Lennox	,,	Not numerous
Peebles-shire	115	Glentress	Roe	Not numerous
	116	Elibank	,,	Occasional
	117	Cardrona	,,	,,
Berwickshire	118	Edgarhope	Roe	Not numerous
Roxburghshire	119	Wauchope	Roe	Not numerous
	120	Tinnisburn	,,	,, ,,
	121	Newcastleton	,,	Numerous
Dumfries-shire	122	Ae	Red	Not numerous
			Roe	,, ,,
			Fallow	,, ,,
	123	Greskine	Red	Occasional
			Roe	Not numerous
			Fallow	Occasional
	124	Castle O'er	Roe	Not numerous
	125	Craigieburn	,,	Occasional
	126	Mabie	,,	Numerous
Kirkcudbright	127	Dalbeattie	Roe	Not numerous
	128	Fleet	,,	Occasional
	129	Laurieston	,,	Not numerous
			Red	Occasional
	130	Garcrogo	Roe	,,
	131	Corriedoo	,,	Not numerous
	132	Dundeugh	,,	,, ,,
	133	Cairn Edward	Red	Numerous
			Roe	Not numerous
	134	Kirroughtree	Red	Numerous
			Roe	,,
	135	Glen Trool	Red	Not numerous
			Roe	Occasional
Wigtownshire	136	Kilsture	Roe	Numerous
Ayrshire	137	Changue	Roe	Numerous
	138	Carrick	Red	Not numerous

* Increasing

STUDIES IN STREAM LIFE IN TRIBUTARIES OF THE WELSH DEE

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(With 1 Figure in the Text)

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1. INTRODUCTION

This study attempts to investigate the fauna of some streams of the Dee river system in Wales, with reference to seasonal variation, food cycles and the available food for the fish population. The field work, apart from preliminary summer samples, extended from September 1946 to July 1947, and involved quantitative studies of the lithophilic fauna in two streams, the Ceirw and the Merddwr, amplified by general collections from various habitats. The gut contents of many forms were investigated and considered in relation to mode of feeding and the constitution of the microscopic planktonic and benthic fauna and flora.

Many of the earlier investigations on the benthic fauna of running waters, both continental and American, are cited by Carpenter (1928) and by Welch (1935). In Britain, the main general surveys of unpolluted waters are those of Carpenter (1927), Percival & Whitehead (1929, 1930), Butcher, Longwell & Pentelow (1937) and Jones (1941, 1943, 1948). Edmonds (1939, unpublished) made an extensive study of the plankton of the Dee, and some observations on the benthos. The chief seasonal quantitative surveys deal with the fauna of a chalk stream (Whitehead, 1935), and of submerged mosses (Frost, 1942). Neill (1938) discusses the fauna of the Scottish Don quantitatively in relation to the food of brown trout. The food of salmon parr has been considered in relation to available fauna of the Eden and Thürso (Allen, 1941) and the Welsh Dee (Carpenter, 1940).

2. METHODS

The three main sampling sites were at Dinmael, a hamlet situated at the confluence of the Merddwr and Ceirw, 5 miles west of Corwen (Fig. 1). The two Ceirw stations (A and B) were below the confluence. Successive samples were collected just upstream (Merddwr A, Ceirw A) or downstream (Ceirw B) from the previous sites and were taken at fortnightly or monthly intervals except when the streams were frozen or too heavily in spate.

Each quantitative sample consisted of the fauna from 2500 sq.cm. of stream bed. Sampling methods which involved removal of large amounts of gravel were not possible owing to transport difficulties. The measured area was marked out with a square frame below which a fine tow-net (129 strands per inch) with an attached jar was placed. Stones were carefully lifted, held in the mouth of the net and rubbed clean. Some organisms were bound to escape because of the swirl, especially during spates. In a few summer samples, this loss was investigated by trapping escaping organisms in an outer cone of mosquito netting with the rim bent so that it formed lateral flaps extending beyond the mouth of the enclosed tow-net (see p. 197). Small forms (below about 3 mm.) were only occasionally retained in either net.

The contents of the nets were washed down into the attached jars, and either preserved in formalin in the field or taken back alive to the laboratory for sorting. All the organisms detected by the naked eye were picked out, sieves (ranging down to 0·5 mm.)

being used when the sample contained much gravel and silt. The animals were identified and counted.

From April onwards, in order to minimize errors due to local distribution, two half samples (each 50 × 25 cm.) were taken at a little distance apart and combined, a procedure discussed by Prebble (1943) for studies of saw-fly populations.

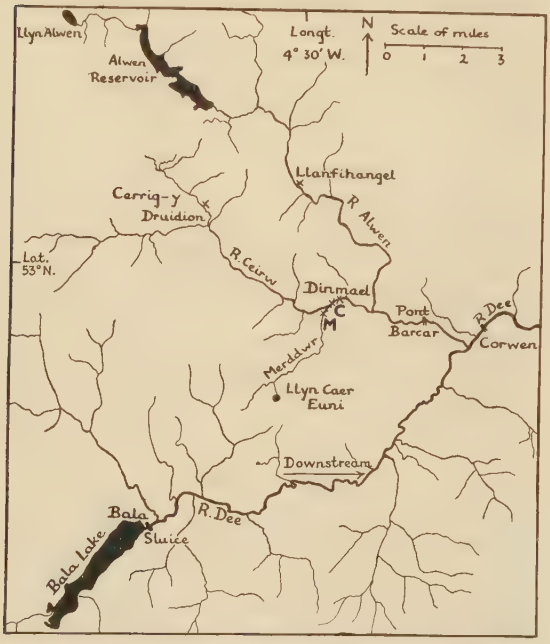

Fig. 1. The upper reaches of the Dee, west of Corwen. C = Ceirw stations A and B. M = Merddwr station A.

Simple physical data obtained at the times of sampling included air and water temperatures, depth of water in the measured area and its average surface velocity, estimated by timing a twig as it floated 20 ft. downstream. The oxygen content of the water was determined by the Winkler method and bromothymol blue was used to indicate the pH.

3. ENVIRONMENTAL CONDITIONS

The Welsh Dee and the tributaries of its upper reaches rise in the hills of Merionethshire and Denbighshire among rocks which are chiefly Ordovician (Bala series, etc.) and Silurian (Caradoc sandstone, Wenlock shales and slates); there are superficial deposits of peat and boulder clay in many places. The sources of the Merddwr, Ceirw and Alwen are in moorland or rough pasture, often boggy, while lower down, these brooks flow through arable or pasture land, partly wooded. There is a small outcrop of Silurian limestone just west of Corwen and a Carboniferous limestone escarpment towers above the Dee at Llangollen, but water of the higher reaches of the Dee and most of its upper tributaries is soft (e.g. Ca as $CaCO_3$—20 mg./l.—Suckling, 1944). The physical history of the valley is discussed by Ramsay (1876).

At Dinmael (550 ft. = 169 m.) the Merddwr is about 4 m. wide and the Ceirw about 7; the beds are mostly stony and unstable, with little vegetation other than mosses on scattered fixed stones. The measured areas were chosen so as to avoid moss. The station Ceirw A was slightly quieter than Ceirw B where the incline was steeper and there were more ripples. Recorded average velocities for Ceirw A range from 30 to 110, for Ceirw B from 45 to 175 and for Merddwr A from 30 to 90 cm./sec. At the nearest meteorological station, Wrexham, the lowest monthly rainfall between September 1946, and July 1947 was 41 mm. (October); peaks were 120 mm. (November) and 160 mm. (March). Depth of water over the various measured areas ranged from 9 to 41 cm. Recorded water temperatures at Dinmael ranged from 0 to 16° C., usually with little difference between the two streams. Ceirw pH values, estimated from water samples collected about noon or in early afternoon, were 7·2 or 7·3 and a single record for the Merddwr was 7·1.

Determinations of dissolved oxygen content of Ceirw water ranged from 9·55 to 16·1 mg./l. at N.T.P., i.e. 87% (at 12·2° C.) to 151% (at 12·8° C.) saturation. Supersaturation was only found on sunny days during the abundance of green algae.

4. THE LARGER BENTHIC FAUNA

(*a*) *Composition of the quantitative samples*

I am indebted to Mr S. T. Burfield and Dr H. B. N. Hynes for checking my identifications of mites and stone-fly nymphs respectively, and to Mr D. E. Kimmins for identifying caddis imagines. I am responsible for other identifications.

Table 1 summarizes the fauna collected in each sample. The population from the stony bed of both streams consisted mainly of insect nymphs and larvae, and is typical of this habitat. Other groups were present in relatively small numbers.

The detailed occurrences of some species of stonefly nymphs are shown in the table; the genus *Leuctra* included *L. fusciventris* Stephens, *L. geniculata* Stephens, *L. hippopus* Kempny and *L. inermis* Kempny. 'Other Plecoptera' comprises infrequent forms such as *Isoperla grammatica* (Poda), *Perlodes mortoni* (Klapálek), *Brachyptera risi* (Morton) and *Protonemura meyeri* (Pictet).

Nymphs of *Baetis*, the commonest Ephemeropteran genus, were not identified specifically. The large nymphs in the winter samples were probably *B. rhodani* (Pictet), but this was not verified by breeding them out. At least two species were present in April,

Table 1. *Numbers of larger benthic organisms in each sample from 2500 sq.cm. of stony stream bed.*

	1946															1947																							
Day and month	11. ix			27. ix			14. x			28. x			16. xii			24. i		15. iv			16. v		13. vi			24. vi			22. vii		
Station	CA	CB	M	CA	CB	M	CA	CB	M	CA	CB	M	CA	CB	M	CA	M	CA	CB	M	CB	M	CA	CB	M	CA	CB	M	CA	CB	M
PLATYHELMIA																																						
Dendrocoelum lacteum (Müller)	2	—	—	—	—	—	1	7	—	—	—	—	—	—	—			1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Polycelis cornuta (Johnson)	—	—	—	—	—	—	—	—	—	—	—	4	—	—	2	—	—	—	—	8	—	1	—	—	—	—	—	—	—	—	—	5
OLIGOCHAETA																																						
Enchytraeidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	28	—	3	17	8	1	2	4	9	6	8	—							
Lumbriculidae	—	—	—	—	—	—	—	—	1	—	—	—	2	—	—	—	—	—	1	10	—	1	3	1	—	1	1	3	—	1	—							
Other Oligochaeta	2	—	—	—	—	1	—	1	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	3	—	—	—	—	—	3	—							
HIRUDINEA	—	—	1	—	—	—	—	—	1	—	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—							
MOLLUSCA																																						
Ancylastrum fluviatile (Müller)	—	—	6	5	—	1	4	4	4	9	—	1	—	—	—	—	—	—	—	1	—	5	4	1	1	—	6	1	2	1	7							
CRUSTACEA																																						
Gammarus pulex (L.)	—	—	2	—	1	8	1	—	12	—	—	1	1	—	8	—	—	—	2	7	—	1	—	—	15	2	1	19	3	—	2							
HYDRACARINA	—	—	—	—	—	—	6	4	8	3	4	1	—	—	—	—	—	5	14	45	—	—	4	4	1	—	3	2	1	—	4							
PLECOPTERA																																						
Perla carlukiana Klapálek nymphs	—	—	—	2	—	—	—	1	2	1	6	—	—	—	—	—	—	1	1	—	2	—	3	2	—	—	6	1	—	—	—							
Chloroperla torrentium (Pictet) nymphs	1	—	—	—	1	15	12	7	1	3	1	7	3	6	1	—	4	7	8	10	5	6	1	2	—	11	1	—	—	—							
Chloroperla tripunctata (Scopoli) nymphs	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—	—	—	—	2	2	2							
**Leuctra* spp. nymphs	—	—	6	—	—	—	—	—	—	—	—	—	7	—	—	—	—	4	7	3	12	4	76	82	6	8	124	51	13	35	16							
Amphinemura cinerea (Olivier) nymphs	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	3	3	—	—	—	—	—	—	—	—	—	—	—	1							
Other Plecoptera and young nymphs	1	2	—	—	—	—	1	—	1	—	1	1	2	—	2	—	—	2	1	4	—	1	1	28	—	1	32	—	2	—	—							
EPHEMEROPTERA																																						
**Baetis* spp. nymphs	9	2	1	1	2	8	27	46	18	17	1	40	18	7	16	12	5	5	24	67	8	15	12	6	2	1	23	43	4	22	57							
Ephemerella ignita (Poda) nymphs	—	—	—	—	—	—	—	—	—	—	—	6	—	—	1	—	—	—	—	—	—	—	16	14	5	5	9	17	16	1	2							
Ecdyonurus nymphs	—	1	2	—	—	5	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	5	1	—	4	—	1	3	1							
Rhithrogena semicolorata (Curtis) nymphs	1	—	—	12	1	2	14	2	1	5	3	1	5	6	2	4	—	9	28	14	11	10	5	—	—	—	1	—	1	—	—							
Caenis nymphs	—	—	—	—	—	—	10	6	4	1	4	1	—	—	—	—	—	12	50	6	2	—	—	5	1	1	4	4	—	—	—							
Young Ephemeropteran nymphs	—	—	—	—	—	1	—	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	—	2	—	4	—	—	—							
TRICHOPTERA																																						
Rhyacophila dorsalis (Curtis) larvae	1	—	2	1	—	—	1	—	—	—	—	—	—	—	—	—	1	—	—	3	—	—	9	7	1	4	4	9	—	—	16							
Rhyacophila dorsalis (Curtis) pupae	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	1	—	—	—	—	—	—	—	—							
Glossosoma boltoni Curtis larvae	—	—	2	—	—	1	3	—	—	3	5	1	1	—	—	2	—	1	5	7	3	2	5	1	—	—	24	6	9	16	8							
Glossosoma pupae	—	—	—	1	—	1	—	—	—	6	1	—	—	—	—	—	1	—	—	—	2	—	4	—	—	1	3	—	1	—	1							
Agapetus fuscipes Curtis larvae	—	—	2	—	—	3	1	—	—	—	—	6	—	—	—	—	—	—	—	1	—	19	—	—	17	—	—	1	—	—	—							
Agapetus pupae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	5	57	—	—	15	—	—	15							
Hydroptilid larvae	1	—	—	—	—	—	5	1	—	4	—	—	1	—	—	—	—	1	1	—	—	—	3	—	—	—	—	—	5	1	—							
Chimarrha marginata (L.) larvae	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	7	—	—	—	5	—	—	3							
Chimarrha marginata (L.) pupae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	—	2							
Polycentropus flavomaculatus (Pictet) larvae	—	—	3	—	—	—	—	—	—	8	—	2	—	—	—	1	—	1	—	1	—	1	3	11	1	1	6	—	5	3	—							
Hydropsychid larvae	—	—	1	—	—	1	—	2	—	1	—	3	1	—	—	—	—	—	3	3	—	—	6	1	1	—	8	4	7	8	5							
Hydropsychid pupae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	1	3	3	—	—	—							
Limnophilid larvae	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	—	—	—	1	—	—	—	—	2	—	—	—	1	—	—							
Goerinae larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	5	1	6	1	—	4	5	—	3	2	—	1							
Silo pallipes (Fab.) pupae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	8	—	11	5	—	4	9	1	11							
Lepidostoma hirtum (Fab.) larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	8	—	1	1	—	2	—	2							
Sericostoma larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	5	6	—	—	—	1	—	—	1	6	4	—	—							
Other caddis larvae	1	—	—	—	—	—	—	—	—	—	—	2	1	—	1	—	—	—	—	2	—	4	—	2	4	1	—	2	4	—	—							
Other caddis pupae or indetermined	—	—	—	3	—	1	1	—	—	—	—	3	—	—	—	—	—	—	—	—	—	1	3	1	4	1	2	—	3	4	—							
COLEOPTERA																																						
Helmid (=elmid) larvae	—	—	2	—	1	—	—	5	—	2	1	—	1	—	—	—	—	8	6	8	—	2	4	1	3	1	17	5	17	13	8							
Helmid (=elmid) and *Hydraena* imagines	—	—	—	—	—	—	—	2	1	—	2	—	2	1	3	—	—	14	16	9	3	3	6	11	—	3	8	5	1	—	1							
Other beetle larvae	—	2	—	—	—	1	—	2	1	1	—	1	—	—	—	—	—	3	—	1	2	—	—	3	—	—	5	—	1	—	—							
Other adult beetles	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—							
DIPTERA																																						
*Chironomid larvae	1	1	6	3	—	5	1	10	5	1	4	18	—	—	—	3	1	19	227	53	42	23	—	269	19	210	605	82	282	51	186							
Simulium spp. larvae	1	1	2	9	5	4	—	10	—	3	—	—	14	—	—	2	—	1	4	11	—	—	—	—	1	—	16	20	—	-	9							
Dicranota larvae	—	—	1	—	—	—	1	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	3	—	—	1	1	1	—	2	—							
Atherix larvae	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	1	2	—	—							
Other dipteran larvae	2	—	1	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	2	1	1	—	—	1							
Dipteran pupae	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	1	5	—	—	—	—	4							
MISCELLANEOUS	—	1	—	1	—	—	—	3	—	—	—	1	—	1	—	—	—	—	—	1	—	1	—	1	—	1	—	1	—	—	2							
Total number of organisms per sample	24	10	40	39	11	45	95	122	71	67	35	94	65	21	42	29	10	102	408	315	101	114	214	506	166	263	924	329	409	175	372							

CA=Ceirw station A, CB=Ceirw station B, M=Merddwr station A.

when imagines of *B. scambus* Eaton were recorded from the area. *Ecdyonurus* imagines captured were *E. venosus* (Fab.) and *E. insignis* (Eaton), but nymphs were mostly *E. venosus*.

The commonest caddis are enumerated specifically in Table 1. No one species was outstandingly abundant. The majority of the Hydropsychidae were *Hydropsyche angustipennis* (Curtis) and *H. instabilis* (Curtis), but larvae and pupae of *Diplectrona felix* McLachlan were recorded in July. Hydroptilids were mainly *Hydroptila* sp. Limnophilids were represented by *Stenophyllax stellatus* (Curtis), *Halesus* and *Apatania*; and Goerinae by *Silo pallipes* (Fab.) and *Goera pilosa* (Fab.) The term 'other caddis larvae' in Table 1 includes the following less frequent forms: *Glossosoma vernale* (Pictet), *Agapetus comatus* (Pictet), *Odontocerum albicorne* (Scopoli), *Notidobia*, *Leptocerus* and *Plectrocnemia*. 'Other caddis pupae' includes *Polycentropus*, *Odontocerum albicorne*, *Lepidostoma hirtum* (Fab.), *Leptocerus* and limnophilids.

The prevalent adult beetles were the helmids [=elmids]: *Esolus parallelopipedus* (Mueller), *Latelmis volkmari* (Panzer) and *Limnius tuberculatus* (Mueller), and the hydrophilid, *Hydraena gracilis* Germar. The helmid larvae included both flattened forms with marginal hairs and cylindrical forms. 'Other beetle larvae' included gyrinids and four rarer types not correlated with their adults.

The Chironomidae included representatives of the Tanypodinae (*Pentaneura* spp.), Chironominae (*Endochironomus* and *Tanytarsus* groups), Diamesinae, Orthocladiinae and an occasional ceratopogonid. Specific identification of *Simulium* larvae was uncertain in preserved material, when the colour pattern on the head is not reliable. *S. tuberosum* Lundstroem larvae and flies were prevalent in June and July, and it is thought that December larvae were this species. *Dicranota* was the commonest tipulid, but *Pedicia* (included under 'other dipteran larvae') occurred sporadically, and so did the leptid *Atherix*. Other larvae were rare.

The few leeches found were *Glossosiphonia complanata* (L.) and *Herpobdella octoculata* (L.). Hydracarines identified were *Atractides anomolus* Koch, *Hygrobates longipalpis* (Hermann), *Lebertia stigmatifera* Thor, and *Pseudosperchon verrucosus* (Protz). The term 'Miscellaneous' includes adventitious and very rare forms.

(*b*) *Distribution as indicated by quantitative samples and general collections*

Polycelis cornuta was the predominant Triclad in the smaller stream, the Merddwr, and *Dendrocoelum lacteum* in the Ceirw, but *D. lacteum* also occurred in the Merddwr. Oligochaetes were apparently very scarce, except for Lumbriculidae and Enchytraeidae, which tend to be associated with stones. Some forms may have escaped by burrowing in the gravel, but the absence of very close moss clogged with detritus and silt probably accounts for the rarity of Naididae. Soft water, dearth of aquatic phanerogams and molar action in floods may account for the paucity of molluscs. *Ancylastrum fluviatile* can tolerate a low calcium content (Boycott, 1936), but it was not very common even on clean stones and was absent where a muddy crust on the stones would prevent adhesion and block the mantle cavity.

Gammarus pulex reproduces at all seasons, but young stages are especially prevalent in summer. Some individuals were infested internally with the orange larva of the acanthocephalan *Polymorphus minutus* Goeze. *Gammarus* and water mites were most numerous in sheltered niches with silt or in moss.

The predominantly carnivorous perlid and perlodid nymphs were not very numerous. *Perla cephalotes* Curtis was very rare compared with *P. carlukiana*—the former is associated with a stable and the latter with an unstable substratum (Hynes, 1941). *Chloroperla torrentium* was relatively common; it eats smaller animals and more detritus (Hynes, 1941). *Leuctra* nymphs, especially *L. fusciventris*, were very abundant during late spring and summer. A few young nymphs (under 3 mm.) of this species were found in April and May; in June, nymphs 4 mm. long were retained in numbers. Numbers decreased by the end of July, probably due to emergence, and only a few fully grown nymphs were found in September. *L. geniculata* nymphs (3–5 mm.) were first recorded in mid-June, there were more at the end of the month, mostly about 5 mm. long and they were common in July. The tendency of *L. geniculata* nymphs to dwell under boulders (avoided in selection of sampling sites) and in deeper water than *L. fusciventris* (Hynes, 1941) would influence the relative abundance in the samples. The prevalent species between December and May was *L. hippopus*. *L. nigra* (Olivier) was found in sheltered situations. *L. inermis*, *Brachyptera risi* and *Isoperla grammatica* were more frequent in the higher reaches of the Merddwr than at Dinmael. *Protonemura meyeri* was only numerous in moss.

Baetis nymphs (not specifically identified) were very common at Dinmael, and dispersal of young nymphs in the plankton is frequent, especially in spring. Nymphs of *Ephemerella ignita*, only recorded in June and July samples, constituted the greater part of the well-developed ephemeropteran nymphs when the baetids were emerging and the new generations hatching, but *Ephemerella* never reached the peak figure for *Baetis*. Its absence from samples before June agrees with observations that *Ephemerella ignita* has a long incubation period (Percival & Whitehead, 1928), and that from November to May the population consists chiefly of small nymphs (1–3 mm.) (Frost, 1942). *Ecdyonurus* nymphs were

less frequent than those of *Rhithrogena semicolorata* in Dinmael samples, especially during winter when they were rarely recorded in the Ceirw, which is liable to spates. Young *Ecdyonurus* nymphs still with strap-like gills were recorded in October and June, which agrees with Rawlinson's (1939) demonstration of two broods a year. The small, rather delicate *Caenis* nymphs were not very numerous amongst stones and gravel except in April, when many small nymphs (1–2 mm.) occurred in the samples.

Agapetus fuscipes, a caddis typical of the quieter niches of stony streams, was much commoner in the Merddwr than in the frequently swifter Ceirw. October larvae were all young, sizes varied in May and June, when pupae were also found. This species is probably univoltine (Whitehead, 1935). *Glossosoma boltoni*, with its larger, more robust case, frequents stones in both streams and overwinters both as immature larvae and pupae. No account of its life history or of that of *Rhyacophila dorsalis* has been seen. Pupae of *R. dorsalis* were collected between April and September, and larvae of varying sizes at all seasons. These caseless larvae, using their stout grappling claws for anchorage, creep about the stony stream bed in the current or cling to moss. In the laboratory, they have been observed swimming with an undulating movement.

Dense populations of the larvae of *Polycentropus flavomaculatus* are associated with gently flowing waters, and amongst stones the rather fragile nets are most numerous where there is a slight deposition of silt indicating quiet conditions, such as are often correlated with lake outflows. These larvae also frequent the stony but slightly silted shores of lakes where there is little wave action but sufficient aeration. At Dinmael *Polycentropus flavomaculatus*, *Hydropsyche angustipennis* and *H. instabilis* spin their nets underneath stones. The life histories are incompletely known and are being studied for a further paper on the biology and ecology of net spinning and caseless caddis.

Notidobia larvae dwelt amongst stones in the Ceirw, Merddwr and Alwen, especially in quiet regions with slight silting, and amongst water weeds.

The philodinid rotifer, *Embarta laticornis* (Murray), was epizoic on larvae of *Halesus digitatus* (Shrank) among *Myriophyllum* and dwelt in the cases (made of fragments of the weed) of very young limnophilid larvae. As it was not found free in samples of the weed, a definite association of this rotifer with the caddis can be established. Murray (1905), who found it among mosses, considered that its form suggested a parasitic habit, but had not then discovered it attached to any host. Mr A. L. Galliford, who kindly identified this rotifer for me, says he has since found it on caddis from Hatchmere, Cheshire, and Dr Slack tells me that *Halesus* and *Silo* larvae from the River Test, Hampshire, sometimes had a philodinid rotifer associated with them.

Beetles were never abundant in the quantitative samples; they are commoner in sheltered moss than among stones (Percival & Whitehead, 1929). Only imagines and larvae were recorded, the pupae are terrestrial.

The numbers of chironomid larvae varied greatly in different samples, and are discussed below. *Simulium* larvae clustered on some boulders in ripples, but were not numerous in the quantitative samples.

(*c*) *Discussion*

The quantitative samples were from one major type of botton habitat—the loose stones devoid of larger vegetation—which is poor in numbers of individuals compared with moss (Percival & Whitehead, 1929), but supports forms—such as *Baetis*, *Ecdyonurus*, *Ephemerella*, many stone-fly nymphs, *Simulium* and chironomid larvae and *Ancylastrum*—which are readily eaten by salmon parr (Carpenter, 1940, Allen, 1941). Much of the fauna living within the gravel was not taken, but it is of little importance as food for salmonids.

The crude sampling method could not be expected to collect the whole bottom population of the measured area, even exclusive of the forms which readily burrow; escape of animals was bound to occur because of the swirl at the mouth of the net. The loss was greatest in floods, and in November the swirl was so strong that practically all the organisms were lost and sampling had to be abandoned.

A typical result obtained during summer for the inner net (the contents of which alone were considered in the quantitative result) and the larger outer net of mosquito netting used to estimate the loss is shown in Table 2. When for each of five samples, the numbers in the outer net were expressed as percentages of the total for both nets it was found that the loss, as estimated by the outer cone, ranged from 4 to 20%. Analysis shows that a wide range of organisms is lost and not merely the smaller forms, some of which might pass through the outer net. Even considering only the variability of total loss, it is apparent that only the most general conclusions may be drawn from a study of the numbers of organisms in the quantitative samples (Table 1).

Any examination of the lithophilic animal population reveals that its distribution is very irregular. Table 1 shows this clearly, especially if the figures are compared for Ceirw A and Ceirw B, stations which are close together and very similar. Hence the necessity for caution in deriving any conclusions from the figures themselves, a point also emphasized by the work of Mottley, Rayner & Rainwater (1938). Leonard (1939) likewise showed the great variation

in the composition of the fauna, although the total volume of organisms present in a given area was more consistent. As an animal population is so variable both seasonally and in its spatial distribution, especially in such a very diversified environment as the bed of a stony stream, only very large numbers of simultaneous samples could be expected to give adequate statistics on the general density of population at one time and place. Also sampling, except at very short intervals of time, could not reflect any but the grossest seasonal changes in the population.

Table 2. *Quantitative yield of sample from Ceirw B on 24 June 1947*

	Inner net	Outer net
Enchytraeid Oligochaetes	4	4
Lumbriculid Oligochaetes	1	2
Ancylastrum fluviatale	6	—
Gammarus pulex	1	—
Hydracarines	3	—
Perla Carlukiana nymphs	6	1
Chloroperla torrentium nymphs	11	1
Leuctra nymphs (*L. fusciventris*, *L. geniculata*)	124	4
Various young Plecopteran nymphs	32	—
Ecdyonurus nymphs	4	—
Rhithrogena semicolorata nymphs	1	—
Caenis nymphs	4	2
Ephemerella ignita nymphs	9	4
Baetis nymphs	23	2
Rhyacophila dorsalis larvae	4	—
Glossosoma boltoni larvae	24	3
Polycentropus flavomaculatus larvae	6	-
Hydropsyche angustipennis larvae	8	—
Silo pallipes larva	—	1
Lepidostoma hirtum larva	1	—
Sericostoma larva	—	1
Caddis larvule (undetermined)	1	—
Glossosoma pupa	3	1
Hydropsychid pupae	3	—
Goera pilosa pupa	1	—
Odontocerum albicorne pupa	1	—
Esolus parallelopipedus imagines	6	—
Latelmis volkmari	—	1
Oreodytes rivalis Gyllenhal	—	1
Other adult beetles	2	—
Helmid larvae	7	—
Dryopid larvae	5	—
Simulium larvae	16	—
Chironomid larvae	605	3
Chironomid pupa	—	1
Dicranota larva	1	—
Pedicia larva	1	—
Adult Diptera	—	2
	924	34

Loss = 4 % of total

Most of the categories of organisms are not represented in any of the samples (except perhaps one) by numbers greater than 25. Those forms which are represented by a greater density of population (starred in Table 1) are *Leuctra* spp., *Baetis* spp. and the Chironomidae. Most of the unstarred forms in Table 1 are represented by numbers much lower than the arbitrarily chosen figure of 'over 25 individuals per 2500 sq.cm.' The list of abundant forms would not have been greatly increased had the chosen number been 'over 15'. Organisms falling into this intermediate group are: Enchytraeidae, *Ephemerella ignita*, *Glossosoma boltoni*, *Agapetus fuscipes* and *Simulium*. Other forms are less numerous.

Two generalizations may be made from analysis of the actual figures in Table 1, namely that the density of population of other forms is markedly lower than that of the starred categories and obviously that their range of variation is much more restricted (0–25). The figures for some of these forms may indicate a seasonal distribution, but the number of samples is too few to establish this for any form, and loss of the smaller individuals from the sampling apparatus leaves open the question of whether seasonal absence from the samples is due to size or to actual absence from the site.

Although the numbers of individuals of a given species may be low, if those of all the members of a higher category, say an order, are added up the importance of some groups becomes obvious. On expressing various groups of animals as percentages of the total population collected quantitatively between September 1946 and July 1947 inclusive, over three-quarters of the population in the Ceirw and Merddwr is seen to be composed of the same four groups (Table 3).

Table 3

	Percentage of total population	
	Ceirw A and B	Merddwr A
Chironomid larvae	48	25
Ephemeropteran nymphs	15	23
Trichopteran larvae and pupae	10	21
Plecopteran nymphs	16	8
Sum of the four groups	89	77

Other groups constitute but a small proportion of the total fauna, each less than 5 % and only very broad generalizations from such figures are considered valid.

From September to January inclusive, the measured area apparently supports a population ranging between 10 and 122 individuals (17 samples); in contrast, the April to July totals lie between 100 and 924 (14 samples). If the chironomid larvae, *Leuctra* and *Baetis* nymphs are deducted, the September to

January range becomes 7 to 66 and that for April to July becomes 39 to 172. The summer increase is due mainly to young insects and especially to the starred categories, the numbers of which vary considerably in different samples, hence actual numbers for seasonal averages (Table 4) are considered to have little value and statistical methods not applicable to the totals. The only statistically significant difference is that between the average total population for summer and winter.

Table 4. *Seasonal averages for total number of organisms per 2500 sq.cm. sample of stony stream bed*

Period	Average	No. of samples and site
Autumn 1946 (Sept. and Oct.)	54	Average of 12 samples— 8 Ceirw and 4 Merddwr
Winter 1946–7 (Dec. and Jan.)	33	Average of 5 samples— 3 Ceirw and 2 Merddwr
Spring 1947 (Apr. and May)	208	Average of 5 samples— 3 Ceirw and 2 Merddwr
Summer 1947 (June and July)	373	Average of 9 samples— 6 Ceirw and 3 Merddwr

The same trend—a fall during winter months and a rise during spring and summer—was found at each of the three stations. In interpreting the winter minimum, the slow growth, small size and hence potential escape of many nymphs and larvae at this season must be remembered; there is also the possibility of their absence not only from the particular measured area but from the stony substratum of all but the most sheltered parts of the stream. This suggestion is supported by the data of Whitehead (1935) correlating a decrease in the lithophilic fauna of a stream with a rise in the population of water weeds at the coming of autumn floods and by the studies of Moon (1934, 1935) and of Berg (1938) showing the considerable movement of the littoral benthic fauna of Windermere and Esrom lakes respectively. The negligible number of chironomid larvae in the Dinmael winter samples is particularly suggestive. The Chironomidae are a very diverse group, but in general they overwinter as larvae, and Frost (1942) found that there was normally a peak (although less than the summer one) of these larvae in moss during winter in the streams investigated by her. Butcher, Longwell & Pentelow (1937) give tables of the fauna from the stony substratum of the Tees which show absence or very low numbers of chironomid larvae in winter. It is unlikely that the April increase at Dinmael was due to growth of new broods, since there was insufficient time for emergence, hatching and growth between the late thaw in April after the exceptionally cold winter of 1946–7 (snow persisted from January to April) and the collection of samples; also, emergence had not been observed. Humphries (1938) showed that in the Grosser Plöner See emergence of chironomids was correlated with temperature, and that the earliest to emerge were some members of the Orthocladiinae at the end of March, when the average temperatures were 7·0° C. (air) and 3·5° C. (lake surface). She cites Lenz as stating that a species of *Paratendipes* is the only form found emerging in winter and then but rarely. Mr P. Freeman tells me that he does not know of any British chironomids which emerge in cold, snowy weather. Thus possibly in a stream which, like the Ceirw, is liable to spates, much of the lithophilic fauna, if not actually destroyed by molar action, is washed or migrates into sheltered habitats such as moss which act as nurseries from which the bare stony substratum is recolonized in spring. Detailed quantitative studies of moss and stone fauna in the same area would be interesting.

The fecundity of an organism and its feeding habits effect its population density. The food chain is considered below: Little is known about the fecundity of many stream forms.

The general collections from various habitats in the Ceirw and Merddwr at Dinmael showed that the quantitative samples gave a representative picture of the population of these streams. Only a few forms were found which were not recorded in the samples. They were:

Ephemera danica Müller nymphs—burrowing in muddy gravel in sheltered situations near the banks.

Leuctra nigra (Olivier) nymphs.

Micronecta poweri (Douglas & Scott)—in shallow silted eddies, nymphs often very abundant.

Velia currens (Fab.)—skating on the surface of eddies.

Calliophrys (Muscidae) larvae—rare and only found in moss.

The fauna at Dinmael is typical of much of the Merddwr, with certain variations. The short narrow outflow gully just below Llyn Caer Euni, the tarn forming the source, is characterized by numerous *Polycentropus flavomaculatus* and *Hydropsyche instabilis*, quantities of *Spongilla lacustris* (L.) and the lacustrine *Leptophlebia vespertina* (L.) instead of *Baetis*. Bivalves, *Pisidium* and *Sphaerium*, rarer downstream, frequented the mud here. *Isoperla grammatica* and *Perlodes mortoni* were more numerous in the upper reaches than at Dinmael, while *Perla* and *Chloroperla* appeared to be absent. On the vertical faces of the rocks of the ensuing waterfall, the fauna is confined to tufts of moss; among bare stones in pools at the base of the falls *Simulium* spp. (including *S. tuberosum* and *S. angustitarsis* Lundström) and *Hydropsyche instabilis* predominated. In the slower middle reaches, the muddy gravel and the weeds *Callitriche*, water crowfoot (*Ranunculus* sp.) and *Myriophyllum* shelter many *Gammarus pulex*, leeches such as *Herpobdella octoculata* and *Helobdella stagnalis* (L.) and numerous limnophilid caddis larvae. The

caddis characteristic of the cleaner, faster reaches were rare, most non-burrowing Ephemeropteran and Plecopteran nymphs were infrequent and mud dwellers such as *Sialis* prevailed. There are areas with a stony substratum, mostly stable, considerable moss* (*Fontinalis antipyretica*, *F. squamosa* and *Hypnum* sp.) and the umbellifer *Oenanthe crocata*, but the greater part of the Merddwr has a looser stony bed and less moss (mostly *Hypnum*) as at Dinmael, and the fauna is very similar to that station.

Incidental collections in the Ceirw above and below Dinmael also revealed a fauna resembling the Dinmael assemblage. More weed occurs in places, also pools which would affect the density of the fauna.

In the upper reaches of the Alwen, immediately below the reservoir and water works' filters, the stones have a flocculent muddy crust. *Hydropsyche* and *Polycentropus* were common, *Dendrocoelum lacteum*, tubificid worms, *Herpobdella* and limnophilid, culicid and chironomid larvae occurred, but Plecoptera and Ephemeroptera were not found. The mucilaginous alga *Palmodictyon*, an occupant of stagnant pools and peaty ditches, was recorded. Above Llanfihangel *Ecdyonurus* and *Isoperla grammatica* occurred, but below it, where the muddy crust was thicker, 'blood worms' predominated, and there was a dearth of larger organisms except for some Limnophilidae and *Polycentropus*. In 1947 the fauna here was not typical of a clean, unpolluted river. Lower down, at Pont Barcar, the fauna was rich and varied as in the Ceirw.

The composition of the fauna at the Dinmael stations seems fairly representative of the clean stony streams of the area and the quantitative studies stress the dominant forms. Only the broadest generalizations can be made from the numbers, and in attempting comparisons with other regions, season and habitats must be carefully considered. Hence detailed comparisons cannot be made with surveys such as those of Jones (1941, 1943, 1948), where collections from many habitats at various times are all added together in presenting the data. As bare, loose stones have been shown by other workers to be much less productive than vegetation, the figures obtained in the present survey probably represent the minimum resources of the Ceirw and Merddwr as food for fish.

5. MICROSCOPIC ORGANISMS

(*a*) *Composition of the flora and fauna*

The only survey of the 'plankton' of the River Dee is that of Edmonds (1939, unpublished) in 1937–8. Studies of river 'plankton' in Britain are not numerous and mostly deal only with phytoplankton. All show its adventitious nature and that much is derived from the benthos. Investigations of the benthic microscopic organisms have also been mainly confined to the algae, microfauna being largely an untouched field, although Picken (1937) discusses communities of ciliate Protozoa in the River Cam.

In the present study, five types of habitat were investigated in varying detail. They were the stones, mud, gravel, moss of the stream and river bed, and the 'plankton'.

Most of the observations were made at Dinmael, and as results in the Ceirw and Merddwr were essentially similar, these stations are considered together. A few additional samples were taken in the Alwen and Dee for comparison. The main difference was in the plankton.

Mr A. L. Galliford kindly identified some of the rotifers.

(1) *Benthos*

In the benthos, especially on stones, diatoms predominated; the genera—with *Cocconeis* frequently the most abundant—resemble those listed by Butcher (1932, 1946) and Butcher *et al.* (1937) and probably represent a typical climax diatom community in such rivers.

Forms recorded were:

Achnanthes
Amphora ovalis Kutzing
Cocconeis spp.
Cymbella spp.
Eunotia
Fragillaria
Gomphonema
Melosira
Meridion circulare (Greville)
Navicula spp.
Nitchia spp.
Stauroneis
Surirella
Synedra spp.
Tabellaria flocculosa (Roth)

The commonest desmids were *Closterium*, *Cosmarium* and *Ankistrodesmus*. Encrusting Chlorophyceae such as *Sphaerocystis*, *Botryococcus*, pleurococcoid forms and *Gongrosira* were characteristic of the stones and particularly abundant in spring. Filamentous Chlorophyceae, clustering in sheltered positions during summer, were represented mainly by *Ulothrix*, but also by *Chaetophora*, *Stigeoclonium*, *Mougeotia*, *Zygnema*, *Oedogonium* and *Spirogyra*. Common blue-green algae were *Nostoc* and the tangled filaments of *Oscillatoria*, which entrapped silt, so forming a muddy crust on stones in quiet regions during the spring abundance. *Chantransia* was the prevalent red alga, but *Hildenbrantia** imparted a dark olive-green slime to some stones and the tough, greenish filaments of *Lemanea** also occurred.

* Kindly identified by Dr E. M. Burrows.

The microscopic fauna dwelling on stones devoid of algal filaments or moss was scanty. The scrapings were either examined on a slide in the field or stored in tubes. Protozoa consisted mainly of occasional representatives of forms more numerous in other habitats. The small oligochaete, *Aelosoma hemprichii* Ehrenberg, and the rotifers, *Philodina roseola* Ehrenberg, *Cephalodella* and *Euchlanis*, occurred on some stones.

In the mud samples examined, diatoms were very numerous and were sometimes mixed with fragments of filamentous algae. Minute green flagellates were the commonest Protozoa, but colourless forms and various hypotrichous ciliates were present. *Difflugia*, diaschizid rotifers and *Pleurotrocha* occurred.

In studying the microscopic organisms of gravel, the most successful method was sucking up a little liquid using a douche syringe with the nozzle pressed well down among the gravel. The material was examined in the field immediately on collection and also after culture. Diatoms loose in the gravel were less numerous than in scrapings from stones but the forms were similar except that the encrusting *Cocconeis* was rarer. Desmids and fragments of algal filaments were present. The protozoan fauna was richer than that obtained from stones. Records included:

Sarcodina
- Actinophrys
- Actinosphaerium
- Arcella
- Difflugia

Mastigophora
- Chrysomonads
- Heteromita ovata Dujardin
- Minute colourless forms

Ciliophora
- Colpidium
- Colpoda
- Euplotes
- Glaucoma
- Holophyra
- Leucophrys patula Ehrenberg
- Liotonopsis
- Oxytricha
- Uroleptus musculus O. F. Müller
- Vorticella

The rotifers *Cephalodella*, *Lepadella*, *Monostyla* and philodinids were found. Gastrotricha were rare in this habitat, but *Chaetonotus* was recorded, so were free-living nematodes.

The microscopic fauna of moss was the richest of all the habitats examined. The forms identified are listed below:

Sarcodina
- Amoeba proteus Rose
- Arcella Ehr.
- Actinospaerium Stein
- Actinophrys Ehr.
- Difflugia Leclerc

Mastigophora
- Chlamydomonas Ehr.
- Euglena viridis Ehr.
- Heteromita ovata Dujardin
- Monas sp.
- Peranema Dujardin

Ciliata Holotricha
- Colpidium colpoda Ehr.
- Glaucoma sp. or near ally
- Lembadion bullinum Perty
- Holophyra Ehr.
- Lacrymaria Ehr.
- Lionotus wrzesniowskii Kent
- Liotonopsis Conn
- Loxophyllum Dujardin
- Trachelius ovum Ehr.

Ciliata Hypotricha
- Euplotes Ehr.
- Holosticha Wrzesniowski
- Oxytricha fallax Stein
- Ophrydium Ehr.
- Urostyla Ehr.
- Vorticella

Rotifera, especially bdelloid forms, are known to be numerous in moss and Mr A. L. Galliford identified the following species from the Merddwr:

- Cephalodella eva (Gosse)
- C. forficata (Ehr.)
- C. tenuior (Gosse)
- Lepadella acuminata (Ehr.)
- Philodina flaviceps Bryce
- Proales reinhardti (Ehr.)
- Proalinopsis sp.

Philodina roseola Ehr. also occurred in this habitat. Other organisms recorded were *Chaetonotus*, *Macrobiotus*, *Aelosoma hemprichii*, free-living Nematoda and larval Hydrachnidae. The diatoms and desmids were the same genera as in other benthic habitats.

(2) *Potamoplankton*

In collecting 'plankton' samples, a fine tow-net, weighted so that it was just below the surface of the water, was suspended in the river for 15 min. Hauls at Dinmael consisted largely of diatoms and plant debris. The diatoms were the typical benthic ones, except that *Cocconeis* was rare. Mingled with them were *Ankistrodesmus*, *Closterium* spp., *Cosmarium* and fragments of green forms which were especially frequent in the plankton in summer and after autumn floods. *Pandorina* and *Sphaerocystis* were recorded. Protozoa were represented mainly by a few individuals of some of the benthic forms. Rotifera were varied but not numerous; the following forms were identified by Mr A. L. Galliford:

- Cephalodella tenuior (Gosse)
- Dicranophorus
- Keratella cochlearis (Gosse)
- Lepadella acuminata (Ehr.)

L. triptera (Ehr.)
Microcodides chlaena (Gosse)
Monostyla lunaris (Ehr).
Notholca longispina Kellicott
Philodina sp.

Cephalodella tenuior and *Lepadella triptera* are characteristic bog forms which probably entered the plankton in the higher reaches of the Ceirw. Copepoda were rare, but species of *Cyclops* and *Canthocamptus* were found occasionally. Ostracoda were very rare. A considerable range of insect nymphs and larvae appeared in the 'plankton' at times, especially in spring, when juvenile forms were common. In summer there were larval mites also.

The few 'plankton' hauls taken in the Dee fall into the general pattern demonstrated by Edmonds during her continuous survey at the same collecting sites in 1937–8. These were Bala Sluice, Corwen Bridge and Farndon, named in order progressing downstream. The composition of the 'plankton' contrasted markedly with the tributary streams where it was characterized by its paucity, especially of zoöplankton and where seasonal variation, except in the Chlorophyceae was not very pronounced. As shown by Edmonds, the water flowing into the Dee from the Bala Sluice gate brings with it many forms from Bala Lake, including a very rich zoöplankton having definite seasonal variation, also lacustrine algae such as the abundant *Asterionella gracimilla* Heiberg and *Coelosphaerium naegelianum* Unger, in addition to forms from the river bed. Some forms were recorded at all Dee stations, the frequency of others such as *Ceratium hirudinella* Müller, *Keratella cochlearis*, *Notholca longispina*, *Filina longiseta* (Ehr.), *Daphnia longispina* (Müller), *Diaphanosoma brachyurum* (Lieven) decreased downstream, while others such as *Leptodora Kindti* (Focke) were recorded only at Bala. At Corwen Bridge, the 'plankton' was still very much richer and more varied than in the Ceirw and Alwen.

(*b*) *Discussion*

These observations illustrate the heterogeneous nature of stream and river 'plankton'—a feature noted by many workers, including Edmonds in her survey of the Dee—and especially the close interrelationship with the benthos. In the Ceirw and Merddwr, the chief difference between the planktonic and benthic microscopic organisms lies in the paucity in the 'plankton' of firmly attached, encrusting forms such as *Cocconeis* and *Gongrosira*. The predominance of diatoms is often characteristic of clean streams. It seems that microscopic organisms are the keystone of biological productivity, but that while in a lake the plankton may be of major importance, in a small stream its role may be played by the benthos. The importance of the age of the water

$$\left(\frac{\text{distance from source}}{\text{velocity}}\right)$$

in determining the nature and quantity of river plankton has been discussed by Kofoid (1903) and Eddy (1934). The influence of a lake on the amount of zoöplankton is obvious when the abundant 'plankton' of the Dee below Bala Lake is compared with the paucity of the tributaries.

Protozoa were investigated in the field whenever possible, immediately on return to the laboratory and in culture. Since forms from fast-flowing unpolluted streams are accustomed to highly oxygenated conditions, the most satisfactory culture method was to have just a little stream water in a large jar so that plenty of air was available and there was a large surface for gaseous exchange. Otherwise many forms disappeared, the culture quickly passing through a hypotrichous ciliate (e.g. *Uroleptus*) to a *Colpidium* association.

On stones, the protozoan fauna was sparse; that amongst gravel, especially under stones, was richer, but of the habitats examined the greatest variety and density was found sheltering in moss.

Picken (1937) correlated abundance of ciliates with plenty of interfaces enabling accumulation of food substances and providing a surface to which the Protozoa could become 'bound'. He found the densest ciliate populations associated with filamentous growths.

This preliminary survey of the microscopic organisms serves to give some indication of the range of forms available in the various habitats.

6. NOTES ON THE FOOD OF THE LARGER ORGANISMS

In order to study the inter-relationships of the fauna, the food of many animals found in the streams at Dinmael was studied and literature relating to such forms surveyed. The organisms were examined either immediately on collection or were preserved in the field. The results are summarized in Table 5.

(*a*) *Invertebrates*

Percival & Whitehead (1929) list the food of a wide range of benthic invertebrates from the Wharfe, and summarize the results in a general food chain. They note that while there is a definite association between *Glossosiphonia* and certain molluscs, *Herpobdella* is much more clearly associated with tubificids and chironomids and may be numerous where molluscs are absent (cf. Richardson, 1928). At Dinmael, *Herpobdella* fed chiefly on chironomid larvae which were often swallowed whole. Tubificids, rare in the

Table 5. *Gut contents of some of the organisms from the streams at Dinmael*

Organism	Months when examined	Number examined	Gut contents: Mineral particles	Diatoms and desmids	Other encrusting algae	Filamentous algae	Pulverized masses	Protozoa	Chironomid larvae	*Simulium* larvae	*Leuctra* nymphs	Indetermined Plecoptera	*Baetis* nymphs	Other Ephemeropteran nymphs	*Hydropsyche* larvae	*Rhyacophila* larvae	*Chimarrha* larvae	Adult Diptera	Entomostraca	Collembola	*Micronecta poweri*
Herpobdella octoculata	viii, ix	10	.	.	.	.	.	.	○	○	.	.	○	.	.	.	.	.	.	.	.
Ancylastrum fluviatile		5	○	○	○	○	.	○	.	.	.	.	.	.	.	.	.	.	.	.	.
Gammarus pulex	iv, v, viii	17	.	○	○	○	.	○	○	.	.	.	.	○	.	.	.	.	.	.	.
Perla carlukiana nymphs	vii	5	.	.	.	○	.	.	○	○	.	.	○	○	○	.	○	.	.	.	.
Baetis spp. nymphs	vii	12	.	○	○	.	.	○	.	.	.	.	.	.	.	.	.	.	.	.	.
Ecdyonurus venosus nymphs	ii, v	5	○	○	○	○	.	○	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhithrogena semicolorata nymphs	ii, v	10	○	○	○	○	○	○	.	.	.	.	.	.	.	.	.	.	.	.	.
Ephemerella ignita nymphs	vii	5	.	.	○	○	.	.	○	.	.	.	.	.	.	.	.	.	.	.	.
Micronecta poweri nymphs	xi	14	○	.	.	.	○	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Glossosoma boltoni larvae	x, iv, vi	12	○	○	.	.	○	○	.	.	.	.	.	.	.	.	.	.	.	.	.
Chimarrha marginata larvae	v	5	.	○	○	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Notidobia larvae	iv, v	5	.	.	.	○	.	○	○	.	.	.	.	.	.	.	.	.	.	.	.
Stenophylax stellatus larvae	iv, vii	5	○	○	.	○	.	.	○	.	.	.	.	.	.	.	.	.	.	.	.
Hydropsyche larvae	Various	18	○	○	.	○	.	○	○	.	.	.	○	.	.	.	.	.	.	.	.
Rhyacophila dorsalis larvae	iv, vii	10	.	.	.	.	.	.	○	○	.	○	○	.	○	.	.	.	.	.	.
Polycentropus flavomaculatus larvae	iv, vii	12	.	.	.	.	.	○	○	○	.	.	○	○	.	○	.	.	.	.	.
Helmid larvae	vii	5	.	○	○	.	.	○	.	.	.	.	.	.	.	.	.	.	.	.	.
Chironomid larvae (excluding Tanypinae)	vii	12	.	○	.	○	.	○	.	.	.	.	.	.	.	.	.	.	.	.	.
Simulium larvae	vii	12	.	○	○	○	○	○	○	○	.	.	.	.	.	.	.	.	.	.	.
Salmo salar fry (2·6–2·8 mm.)	iv–vi	23	.	○	.	○	.	.	○	○	.	.	○	.	.	.	○	○	○	○	.
Phoxinus phoxinus (2·0–2·9 mm.)	v	15	.	○	.	○	.	○	○	.	.	.	○	.	.	.	○	○	○	○	.

○ denotes presence, ○ ○ predominance.

fauna, were not found in the guts of these leeches, but *Baetis* and *Leuctra* nymphs were sometimes eaten. *Ancylastrum fluviatile* had been scraping stones (see Boycott, 1936). The varied assortment of detritus which *Gammarus pulex* had eaten included bits of plant tissue, diatoms, other algal cells and also much mineral matter; insect remains, especially chironomid larvae, were sometimes found. These results agree with those of Percival & Whitehead and partly with the generalization of Embody (1911) that fresh-water gammarids eat both living and dead plants and animals. *Gammarus* is known to eat dead leaves (cf. Sexton & Matthews (1913) on *G. chevreuxi*), and in one of the *G. pulex* examined brown pieces of leaf were the only gut contents.

At Dinmael, the only Plecoptera examined for their gut contents were large *Perla carlukiana* nymphs and they had eaten a wide range of insect nymphs and larvae. Grau (1926) systematically studied the food of perlid stone-fly nymphs, showing that they ate animals and algae, Claassen (1931) and Küktreiber (1934) established the main differences between the carnivorous and phytophagous types of mouthparts, and Hynes (1941) studied the food of the two groups Setipalpia and Filipalpia.

Observations on *Ecdyonurus venosus* confirmed the range of herbivorous food described by Rawlinson (1939), while *Rhithrogena semicolorata*, with essentially similar mouthparts and mode of feeding, also brushed up encrusting algae, diatoms, morsels of plant tissue and, in summer, fragments of filamentous algae. It is not known whether the inclusion of filamentous algae is necessary for the growth of *Rhithrogena* as has been suggested in the case of *Caenis* (Moon, 1938). The form of the mouthparts and gut contents of *Baetis*, in which *Cocconeis* valves and plant tissue predominated, suggests that these nymphs both scrape and bite. The relatively large, powerful labrum with its considerable range of fore and after movement probably acts as a shovel, while the dissimilar mandibles each have well-developed 'canine' teeth and a ridged area for grinding; the maxillae with bristles and teeth may aid in brushing up and biting food. Even in those nymphs in which *Cocconeis* was most abundant in the fore-gut, it was rare or absent in the hind-gut, a feature which suggests regurgitation from the crop.

The amorphous mass in the crop of *Micronecta poweri* nymphs possibly represented the contents of algal filaments sucked out when these cells are pressed against the rostrum by the palea. There was no definite evidence of pharyngeal mastication as described by Walton (1938).

Several attempts have been made to correlate the food of Trichopteran larvae with anatomical characters of the head. Siltala (1907) concluded that those with brushes of setae on both mandibles were phytophagous, while those with brushes on the left mandible only might be phytophagous, omnivorous or carnivorous and those with no mandibular brushes were carnivorous or omnivorous. Wesenberd-Lund (1911) attempted to correlate the anterior or posterior position of the eyes and relative width of head with a carnivorous or phytophagous habit, a theory to which there are many exceptions as has been shown by Slack (1936). The generalization of Martynov (1930) that the Annulipalpia are mainly carnivorous and the Integripalpia phytophagous by preference is also too sweeping as has been shown by Ahmad (1936, unpublished) in his study of the mouthparts and alimentary canal of many caddis larvae in relation to feeding habits.

Observations of caddis larvae at Dinmael showed that *Glossosoma boltoni* ate diatoms and such other algae as may be included when it is brushing or scraping the surface of stones. The stout mandibles, devoid of teeth, each have a long brush of hairs and the eyes are posterior, so this larva resembles *Silo* in these features and fits into Wesenberg-Lund's theory. The coccoid algae and diatoms selected by *Chimarrha marginata* larvae also indicate a stone-scraping habit, agreeing with Noyes (1914) who found only vegetable food in this species, although the mandibles are strongly developed, have sharp teeth and lack the median tuft of hairs. In *Notidobia*, both mandibles are stout, have brushes of hairs and blunt teeth. Neatly cut-up pieces of fresh plant tissue predominated in their guts, but some algal filaments had been eaten. *Stenophylax stellatus* larvae were predominantly phytophagous.

It is generally agreed that *Hydropsyche* larvae are omnivorous and the predominant food evidently varies with availability and conditions, but the function of the net is controversial. Wesenberg-Lund (1911) considers that it catches food, and Richardson (1921) lists *Hydropsyche* among planktonic feeders in the Illinois. In contrast, Krawany (1929) concluded that in the brook at Lunz the larvae were plant eaters and did not use their nets to catch plankton in streams where moss and algae were prevalent. The presence in the guts of much *Cocconeis*, which was rare in the plankton, and the position of the dwellings under stones seems to indicate that in the Ceirw and Merddwr the food was brushed up from the bottom rather than netted. At Dinmael, the net and dwelling may be of greatest use for anchorage and perhaps protection.

Rhyacophila dorsalis larvae lived up to their 'typically carnivorous' reputation in devouring insect nymphs and larvae. *Polycentropus flavomaculatus* larvae were also carnivorous, demolishing a wide range of young insects and ignoring algae entangled in their nets.

Simulium larvae have been shown by Smart (1944)

to catch particles in the passing current with their mouth brushes. Both he and Wu (1931) note that the larvae may pick up food from the substratum, but consider that this may be an adaptation to starvation conditions in the laboratory. Those studied at Dinmael were predominantly phytophagous, but occasionally ate their own species and chironomid larvae. The abundance of *Cocconeis* in the guts suggests that *Simulium* brush up their food from stones more commonly in nature than Smart and Wu supposed, especially in streams which are not rich in plankton.

While many chironomid larvae eat mainly plant detritus, the entire subfamily Tanypodinae are predacious, feeding especially on 'blood worms' and small crustaceans, although they may also eat the more rapidly moving diatoms (Leathers, 1921). A few observations at Dinmael served to confirm the generalization that forms other than Tanypodinae eat detritus and plant material and are more numerous than the carnivorous genera.

(*b*) *Fish*

These Welsh streams are considered by anglers and the river bailiffs to be well stocked with brown trout (*Salmo trutta* L.), the natural population having been augmented with many 4–8 oz. fish. Planting out of salmon fry is also practised and there is quite a good natural population of salmon (*Salmo salar* L.). Minnows (*Phoxinus phoxinus* (L.)) are common and eels (*Anguilla anguilla* (L.)), loach (*Nemachilus barbatula* (L.)) and bullheads (*Cottus gobio* L.) are known to be present.

The food of older salmon and trout has often been studied, but fish under 1 year have received little attention, especially in Britain. Salmon fry (lengths 2·6–2·8 cm.) were obtained from the Pont Barcar hatchery tank which had a gravel bed and service pipe line from the river. It resembled a fairly natural lotic environment augmented by an occasional plankton haul from a neighbouring lake. While the intestine contained yolk, the fry mostly rested under stones unless disturbed and, although the mouth was open, the ones examined were not feeding. In later stages when the yolk was exhausted, the fish came out into the open and started devouring chironomid and *Simulium* larvae, also algae such as *Ulothrix* and *Stigeoclonium* filaments, *Synedra* and monads. Small flies, *Baetis* nymphs and collembolans were occasionally taken. Chydorids and *Canthocamptus* from lake plankton were acceptable and, in contrast to minnows, the salmon fry took nymphs of *Micronecta poweri* when these were offered. The diet of a couple of fry of this size caught in the Ceirw resembled that of the fish from the tank except for the absence of lacustrine organisms. Larger fry (4–5 cm.) from the stream had a wider range of diet, additions including *Leuctra* and *Ephemerella* nymphs and adult helmid beetles. This agrees with White (1936) in eastern Canada, who concluded that while smaller fry select smaller organisms such as chironomid larvae and minute pupae, probably the general character of the food is decided largely by its daily availability, a conclusion also arrived at by Carpenter (1940) for salmon parr, and Neill (1938) for trout. Salmon parr eat a variety of organisms (Carpenter, 1940; Frost & Went, 1940; Allen, 1941) and so do brown trout (Pentelow, 1932; Slack, 1934; Neill, 1938; Allen, 1945). As the fish grow larger, Ephemeropteran nymphs and chironomid larvae are eaten less, caddis larvae and molluscs become more accessible. A few observations on trout from the Alwen confirmed this wider range of diet in larger fish.

The food of the young minnows studied was varied (Table 5), and agreed with that found by Frost (1943) in the River Brathay except that diatoms were of more importance than in her fish of corresponding size. Frost points out, after considering all age groups of minnows, that in running waters the food requirements closely coincide with those of salmonids and that the possibility of serious competition is great. My observations on the food of salmon fry emphasize this similarity in the young stages. The eel is another potential competitor since it eats insect larvae (Frost, 1946) and may even prey on salmonids. Bullheads and loach devour some of the same organisms, as they feed on insects and Crustacea (Hartley, 1948).

7. FOOD-CHAINS AND THE STREAM COMMUNITY

This discussion should start at the level of water analyses, bacteria, microscopic flora and Protozoa. The nutrient and bacterial content of Ceirw and Merddwr waters were not analysed, but as they are well oxygenated and there are many young insects characteristic of unpolluted waters, the dissolved organic matter could not be very great. The mineral content was obviously adequate to support a varied algal flora and also the holophytic Protozoa. The food of Protozoa is reviewed by Sandon (1932), who stresses the importance of specific strains of bacteria, of various small algae including diatoms, and of other Protozoa and rotifers as food for free-living, holozoic forms. Picken (1937) illustrates this with diagrams of the food relationships within ciliate communities in the River Cam. He considers that Protozoa have few metazoan predators, their enemies being mostly other Protozoa. The food of rotifers (cited by Picken as bacteria) is very varied (Wesenberg-Lund, 1929); it consists of many small organisms, both plant and animal, including Protozoa. Owing to the rapidity with which delicate forms such as Protozoa would be digested, it is difficult to determine directly their

importance as food for other organisms and the significance of diatoms with their indigestible tests may be over-stressed. Indeed, these may be swept into the gut together with the actual food, but may not always be utilized. Planktonic investigations which cast doubt on the complete dependence of marine copepods on diatoms are summarized by Clarke (1939), who stresses the need for considering the nannoplankton: this line of thought might well be pursued in fresh-water studies.

In the present survey, the presence of a varied protozoan fauna was demonstrated, especially in moss and amongst gravel, but these forms were rarely detected in the few guts examined. Apart from the impossibility of finding Protozoa in preserved material, it apparently made little difference whether the material was fresh or preserved. Rotifers were rare in the guts studied, except in limnophilid caddis which had evidently ingested their commensals, but they are recorded in the food of *Chloroperla* (Hynes, 1941). Table 5 indicates the apparent importance of algae and other plants as the basis of a food chain, and this emerges still more clearly if the larger members of the stream community are listed under their predominant feeding habits. An asterisk indicates forms for which the findings have been culled only from the literature and the authority is given in brackets.

Predominantly phytophagous forms	Omnivorous forms	Predominantly carnivorous forms
Ancylastrum fluviatile	*Hydropsyche* larvae	*Herpobdella octoculata*
Chironomid larvae excluding Tanypodinae	**Chloroperla* spp. (Hynes, 1941)	*Perla carlukiana* nymphs
Baetis spp. nymphs	*Phoxinus phoxinus*	*Polycentropus flavomaculatus* larvae
Ecdyonurus venosus nymphs	*Salmo salar* fry	*Rhyacophila dorsalis* larvae
Rhithrogena semicolorata nymphs	—	*Hydracarina (Mellanby, 1938)
Ephemerella ignita nymphs	—	**Dicranota* larvae (Miall, 1893)
Micronecta poweri nymphs	—	**Salmo salar* parr
Glossosoma boltoni larvae	—	**Salmo trutta*
Chimarrha marginata larvae	—	**Nemachilus barbatula* (Hartley, 1948)
Notidobia larvae	—	**Cottus gobio* (Hartley, 1948)
Stenophyllax stellatus larvae	—	—
Helmidae larvae	—	—
Simulium spp. larvae	—	—
**Silo* (Siltala, 1907)	—	—
*Enchytraeidae (Stephenson, 1930)	—	—
**Leuctra* spp. nymphs	—	—
**Amphinemura* nymphs (Hynes, 1941)	—	—
**Agapetus* spp. larvae (Percival & Whitehead, 1929)	—	—

The Chironomidae constitute a food chain among themselves, and as the proportions of Tanypodinae and other chironomid larvae were not determined, although it was apparent that the latter were considerably more numerous than the former, the figures in Table 1 cannot be used to demonstrate a pyramid of numbers in detail. It is evident, however, that the predominantly phytophagous species exceed the omnivorous and predominantly carnivorous ones and that all those stone dwellers with the greater population density, say 'over 15', in more than one 2500 sq.cm. sample (Chironomidae, *Baetis* spp., *Leuctra* spp., Enchytraeidae, *Ephemerella ignita*, *Glossosoma boltoni*, *Agapetus fuscipes* and *Simulium* spp.) are predominantly phytophagous.

Thus the invertebrate fauna of the Ceirw and Merddwr is varied and capable of supporting a good population of Salmonidae; with its numerous chironomid larvae and *Baetis* nymphs, it is especially suitable for the rearing of fry.

8. SUMMARY

1. Quantitative samples from the stony bed of some Welsh streams indicate the composition of the fauna and demonstrate the great variability in population density.

2. Immature insects, especially chironomid larvae, *Baetis* and *Leuctra* nymphs, predominate. The occurrence in the samples of various forms is considered in relation to their ecology and life histories.

3. The population of the stony substratum was least dense during winter.

4. A brief survey of the planktonic and benthic microscopic organisms in the streams, and a comparison with the plankton of the Dee itself, indicates the nature of the potential basic food supply. Zoöplankton is sparse in the streams, where the plankton consists chiefly of diatoms derived from the benthos. Moss has a richer microscopic fauna than gravel, mud or stones.

5. The gut contents of many organisms are considered. Forms feeding on algae and plant tissue (especially debris) predominate. Those animals

shown to be most numerous in the samples are detritus feeders or phytophagous. The invertebrate fauna is considered in relation to the fish population, the climax of the food chain in the stream.

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THE HABITS AND ECOLOGY OF THE BRITISH HARVESTMEN (ARACHNIDA, OPILIONES), WITH SPECIAL REFERENCE TO THOSE OF THE OXFORD DISTRICT

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(With Plates 10–12 and 5 Figures in the Text)

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1. INTRODUCTION

Meade (1855, 1861), Simon (1879) and Pickard-Cambridge (1890) give accounts of the habits of harvestmen, together with the places in which they are likely to be found and some idea of their feeding habits. Kästner (1926, 1935) gives a general account of the habits of the European Opiliones along with his studies on the morphology and embryology of the group. Short recent contributions to the ecology of the British species have been made by Savory (1935, pp. 126–42, 1938), Bristowe (1941, pp. 324–5, 382–3) and Ellis (1942). Bristowe (1949) has added further notes on ecology, and gives distribution maps and data for the British species. Goodnight (1946) and O'Brien (1947) have published abstracts on some American species. The only detailed ecological investigation is that by Stipperger (1928) on the biology and distribution of the North Tirol Opiliones. She has listed the Tirol species according to their vertical distribution in the region, and has made some observations on the seasonal development of the different species.

The University's estate at Wytham Woods, Berkshire, was selected as the area for this field study, as it is easily accessible from Oxford, and offers a variety of habitats, which range from wet marshland to climax oak woodland.

2. FIELD WORK

(*a*) *Description of the area*

Wytham Great Wood is some 4½ miles north-west of Oxford, where it lies in a triangle bounded by the River Thames on the north-west and north-east, and by the Oxford–Witney road on the south. With an area of about 900 acres the estate is part woodland and part open or scrub-covered common land. Most of the present research was done on the north hill. Acknowledgement is made to the University authorities for permission to carry out this study on the estate.

(1) *Geology*

The wood is on rocks of Jurassic origin in which the Corallian and Oxford Clay series are represented. Wytham Hill (545 ft.), the main topographical feature, is a coralline outlier upon a base of Oxford Clay. Coral Rag, a white fairly compact limetone, occurs from the top of the hill down to approximately

the 450 ft. contour. Calcareous Grit lies below this and outcrops between approximately the 400–450 ft. contour. It is a yellowish grey calcareous sandstone which is very much weathered. Extensive beds of Oxford Clay lie below this. The three layers are tilted gently to the south-east at an angle of about 4 degrees (Hancock, 1946). A superficial deposit of Pleistocene fluvio-glacial Plateau drift is thought by some to fill the depressions of the Coral Rag outcrops on the top of the hill. Others believe this to be derived from the weathering of the Coral Rag itself. Some recent Alluvium from the River Thames enters the wood for a short distance on its north boundary. During late geological time considerable modification of this series has taken place. Particularly on the north face there has been extensive slipping of rocks from the Coral Rag and Calcareous Grit region over the Oxford Clay below.

A line of springs may be mentioned which occurs on the bedding plane of the Calcareous Grit Sand with the impervious Oxford Clay.

(2) *Soil*

In general, the soils follow the underlying strata, except where creep has occurred. This results in a larger area of soils derived from the Coral Rag; there is comparatively little pure Oxford Clay as this, for the most part, is overlain by a mixture of Calcareous Grit sand and clay, which forms a sand clay colluvium.

In this survey the sampling has been confined to the Coral Rag Limestone (CRL) region on top of the hill and the sand clay colluvium (SCC) area. The marshes sampled proceed from the line of springs mentioned. Throughout the paper the abbreviations (CRL) and (SCC) will be used to designate the type of soil of any habitat.

(3) *Climate*

Sampling was carried out during a 12-month period from May 1946 to the end of April 1947. No constant recording of temperature was done in the wood. Records of the temperature, relative humidity and precipitation for this period may be found at the Radcliffe Meteorological Station, Oxford. The ground was covered with snow from the end of January to late in March and no sampling was done during this period. The total rainfall for the 12 months exceeded the normal by 6·77 in.

(*b*) *Description of the plant cover of habitats*

The general woodland of Wytham approximates to Tansley's (1939) damp pedunculate oakwood type, though through the invasion of sycamore (*Acer pseudo-platanus*) this is often much modified. Two conifer plantations, planted in 1920, are among the habitats sampled, which range from a wet *Equisetum* marsh at the bottom of the hill through such places as open bracken and cut-over wood to climax woodland and limestone grassland on top of the hill.

In the following descriptions, which represent the vegetation found immediately round the quadrats sampled, the plants are divided into those in the tree, shrub, field and ground layer. The frequency is denoted by the usual letters d. (dominant), a. (abundant), f. (frequent), o. (occasional), r. (rare) and l. (local).

Habitat 1. Marsh (very wet)

Field layer	Equisetum telmateia	a.d.
	Valeriana dioica	f.
	Epilobium parviflorum	f.
	Eupatorium cannabinum	f.
	Ajuga reptans	f.
	Pulicaria dysenterica	o.
	Scrophularia nodosa	o.
	Filipendula ulmaria	o.
	Orchis fuchsii	o.
Ground layer	Hypnum cuspidatum (and other spp., not noted)	a.

Habitat 2. Marsh. Some Fraxinus excelsior regeneration

Field layer	Carex riparia	a.
	Eupatorium cannabinum	f.
	Epilobium hirsutum	f.
	Ajuga reptans	o.
	Symphytum officinale	f.
	Hypericum elodes	o.
	Angelica sylvestris	o.
	Pteridium aquilinum	o.
	Paris quadrifolia	l.

Ground layer	Eurhynchium striatum	a.
	Plagiochila asplenioides	a.
	Brachythecium rutabulum	f.
	Lophocolea bidentata	f.
	Pellia epiphylla	o.

HABITAT 3. Mixed deciduous wood (SCC). Here there has been invasion by Acer pseudo-platanus

Tree layer	Acer pseudo-platanus	a.d.
	Quercus robur	f.
	Fraxinus excelsior	o.
Shrub layer	Crataegus oxyacanthoides	o.
Field layer	Mercurialis perennis	a.
	Dryopteris filix-mas	f.
	Circaea lutetiana	f.
	Pteridium aquilinum	f.
	Rubus fruticosus agg.	l.f.
	Scilla non-scripta	o.
	Urtica dioica	o.
	Arum maculatum	o.
Ground layer	Eurhynchium striatum	a.

HABITAT 4. Mixed deciduous wood (CRL). Here there has been invasion by Acer pseudo-platanus

Tree layer	Acer pseudo-platanus	a.d.
	Quercus robur	f.
	Fraxinus excelsior	r.
Shrub layer	Sambucus nigra	o.
Field layer	Mercurialis perennis	a.
	Scilla non-scripta	f. (or may be absent)
	Arum maculatum	f.
	Circaea lutetiana	f.
	Sanicula europaea	o.
	Urtica dioica	o.
Ground layer	Porotrichum alopecurum	a.d.
	Eurhynchium striatum	f.
	Eurhynchium praelongum	o.
	Brachythecium velutinum	o.
	Hypnum cupressiforme	May be present on the base of tree trunks

HABITAT 5. Cut-over deciduous wood (SCC)

Tree layer	Acer pseudo-platanus	f.
	Quercus robur	f.
	Fraxinus excelsior	o.
Field layer	Mercurialis perennis	a.
	Glechoma hederacea	a.
	Ajuga reptans	f.
	Primula vulgaris	o.
	Scilla non-scripta	o.
	Arum maculatum	o.
	Urtica dioica	o.
	Viola reichenbachiana	o.
Ground layer	Porotrichum alopecurum	a.
	Thuidium tamariscinum	f.
	Eurhynchium praelongum	o.

HABITAT 6. Cut-over deciduous wood (CRL)

Tree layer	Acer pseudo-platanus	f.
	Quercus robur	o.
	Fraxinus excelsior	o.
Shrub layer	Sambucus nigra	r.
	Acer pseudo-platanus regeneration	f.

HABITAT 6 (*contd.*)		
Field layer	Mercurialis perennis	a
	Circaea lutetiana	c
	Urtica dioica	f
	Epilobium hirsutum	f
	Chamaenerion angustifolium	o
	Senecio jacobea	o
Ground layer	Eurhynchium striatum	a
	Eurhynchium pulchellum	f
	Porotrichum alopecurum	f
	Thuidium tamariscinum	o
HABITAT 7. Bracken (SCC). Oak felled 1000 and 1014–18		
Shrub layer	Acer pseudo-platanus regeneration	o
Field layer	Pteridium aquilinum	a/f
	Anemone nemorosa	c
	Rubus fruticosus agg.	f–a
	Rubus caesius	f–o
	Mercurialis perennis	f
	Ajuga reptans	f
	Chamaenerion angustifolium	f–c
	Euphorbia amygdaloides	f
	Urtica dioica	f
	Epilobium hirsutum	f–c
	Galium aparine	f
	Scilla non-scripta	o
Ground layer	Eurhynchium striatum	a
	Eurhynchium praelongum	c
	Thuidium tamariscinum	f
	Eurhynchium swartzii	o
	Carbamnea undulata	o
	Fissidens taxifolius	o–f
HABITAT 8. Bracken (CRL)		
Shrub layer	Fraxinus excelsior regeneration	o
	Euonymus europaeus	o
Field layer	Pteridium aquilinum	a–c
	Rubus fruticosus agg.	f
	Mercurialis perennis	f
	Urtica dioica	f
	Ajuga reptans	o
	Galium aparine	o
Ground layer	Thuidium tamariscinum	a–d
HABITAT 9. Deciduous scrub woodland (SCC)		
Shrub layer	Prunus spinosa	f.
	Cornus sanguinea	f.
	Salix caprea	f.
	Sambucus nigra	f.
	Lonicera periclymenum	o.
	Salix viminalis	o.
	Ligustrum vulgare	o.
	Euonymus europaeus	o.
Field layer	Rubus caesius	f.
	Mercurialis perennis	a.
	Urtica dioica	f.
	Ajuga reptans	f.
	Glechoma hederacea	f.
	Epilobium hirsutum	f.
	Epilobium montanum	o.
	Paris quadrifolia	l.f.
	Hypericum hirsutum	o.

	Scilla non-scripta	o.
	Dryopteris filix-mas	o.
	Pteridium aquilinum	o.
Ground layer	Eurhynchium praelongum	a.
	Mnium undulatum	a.
	Eurhynchium piliferum	o.

HABITAT 10. Hawthorn hedgerow (mixture of CRL and Calcareous Grit Sand)

Shrub layer	Crataegus monogyna	a.d.
	Sambucus nigra	f.
	Ligustrum vulgare	f.
	Hedera helix	f.
	Clematis vitalba	o.
	Bryonia dioica	o.
Field layer	Arrhenatherum elatius	a.
	Urtica dioica	l.a.
	Mercurialis perennis	f.
	Dactylis glomerata	o.
	Bromus ramosus	o.
	Brachypodium sylvaticum	o.
	Epilobium hirsutum	o.
	Epilobium montanum	o.
	Equisetum telmateia	o.
	Heracleum sphondylium	o.
	Melandrium dioicum	o.
	Galium aparine	o.
	Chaerophyllum temulum	o.
	Arum maculatum	o.
Ground layer	Thuidium tamariscinum	o.

HABITAT 11. Beech wood

Tree layer	Fagus sylvatica	a.d.

HABITAT 12. Conifer wood (Calcareous Grit Sand and SCC)

Tree layer	(1) Pseudotsuga taxifolia	a.d.
Field layer	Mercurialis perennis	l.
	Urtica dioica	l.
	or (2) Larix decidua	a.d.

HABITAT 13. Grassland (SCC)

Field layer	(1) adjoining woodland	
	Dactylis glomerata	a.
	Arrhenatherum elatius	a.
	Urtica dioica	f.
	or (2) open, near river	
	Festuca ovina	a.d.
	Luzula campestris	f.
	Carex flacca	f.

HABITAT 14. Grassland (CRL)

Field layer:	Brachypodium pinnatum	a.d.
	Bromus erectus	f.
	Helianthemum nummularium	f.
	Koeleria gracilis	o.
	Galium verum	o.
	Viola hirta	o.
	Thymus serpyllum agg.	o.–f.
	Poterium sanguisorba	r.
Ground layer	Brachythecium purum	a.d.
	Hypnum cupressiforme	f.
	Hylocomium squarrosum	f.
	Mnium undulatum	f.
	Dicranum scoparium	l.

(c) *Methods*

(1) *Sampling*

Harvestmen are found on the ground (Gr) and field layers (FL), on tree trunks (Tr) and among the leafy branches (Br) of trees. The sampling of a habitat was carried out in an endeavour to include any of these microhabitats that were present in it.

A square metre litter sample was taken at random on the ground. Harvestmen on the surface were approximately equal area were beaten and the resulting animals collected in a tray.

In the laboratory the material was sorted, determined and catalogued. The litter sample was placed on sieves in Tullgren funnels for 12–24 hr., depending on the dampness of the sample. In the funnel, a 100 W. bulb was suspended 4 in. above the litter, which reached a temperature of approximately 28° C. The harvestmen moved down from the light and heat and were collected alive in the container below. This

Table 1. *Habitat distribution*

(× denotes presence)

Species	Habitats 1 Marsh (*Equisetum*)	2 Marsh (*Carex*)	3 Mixed decid. wood (SCC)	4 Mixed decid. wood (CRL)	5 Cut-over wood (SCC)	6 Cut-over wood (CRL)	7 Bracken (SCC)	8 Bracken (CRL)	9 Decid. scrub woodland	10 Hawthorn hedgerow	11 Beech wood	12 Conifer wood	13 Grassland (SCC)	14 Grassland (CRL)	15 Cornfield	16 Oxford gardens
Trogulus tricarinatus (L.)	.	.	.	.	.	.	×	.	.	.	.	.	.	×	.	.
Anelasmocephalus cambridgei (Westw.)	.	.	.	×	×	×	×	×	×	×	×	×	×	×	.	.
Nemastoma lugubre (Müller)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	.	.
N. chrysomelas (Herm.)	.	×	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Homalenotus quadridentatus (Cuv.)	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.
Leiobunum rotundum (Latr.)	×	×	×	×	×	×	×	×	×	×	×	×	×	.	×	×
L. blackwalli (Meade)	×	×	×	×	×	×	×	×	×	×	.	×	×	×	.	×
Nelima silvatica (Simon)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mitopus morio (Fabr.)	×	×	×	×	×	×	×	×	×	.	×	×	×	.	.	.
Oligolophus tridens (C. L. Koch)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	.	×
O. agrestis (Meade)	.	×	×	×	×	×	×	×	×	×	×	×	.	×	.	×
O. hanseni (Kraep.)	.	.	×	×	×	×	.	×	×	×	.	×	.	.	.	.
O. meadei Camb.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	.	.
Odiellus palpinalis (Herbst)	×	×	×	×	×	×	×	×	×	×	.	×	×	×	.	.
O. spinosus (Bosc.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×
Lacinius ephippiatus (C. L. Koch)	×	×	×	×	×	×	×	×	×	×	.	×	×	×	.	.
Phalangium opilio L.	.	.	.	.	.	.	.	.	.	.	.	.	.	×	×	×
Opilio parietinus (Deg.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×
O. saxatilis (C. L. Koch)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	×
Platybunus triangularis (Herbst)	×	×	×	×	×	×	×	×	×	×	×	×	×	×	.	.
Megabunus diadema (Fabr.)	.	.	×	×	×	×	.	.	×	.	.	×	.	.	.	.

removed, the litter or moss, or both, collected and taken back to the laboratory for examination, and the ground beneath the litter searched for further specimens. The field layer was swept with a net, 30 cm. in diameter, with a swing of about a metre. Two samples of twenty-five sweeps each were taken in this way. Where trees were present in the habitat, the harvestmen were collected to a height of 6 ft. from the ten tree trunks (diam. 8–18 in.), nearest to the place where the square metre sample was taken. Four branches of had a base of plaster of Paris which was kept damp, thus providing a positive humidity gradient from sieve to container in addition to the negative heat and light gradient given by the position of the electric bulb.

The number of samples varied from one to four, and was usually one or two a month in each habitat. No sampling was done in February. The square metre sample is the only true quantitative density measure, and the component samples taken in a

Photo V. Todd

Photo 1. Oak-ash-sycamore wood, on sand-clay colluvium, Wytham Woods, Berkshire. (Habitat type 3.)

Photo V. Todd

Photo 2. Woodland spring marsh, with *Equisetum telmateia* and *Eupatorium cannabinum*, Wytham Woods, Berkshire. (Habitat type 1.)

Photo V. Todd

Photo 3. Oak-ash-sycamore wood with *Mercurialis perennis* field layer, on sand-clay colluvium, Wytham Woods, Berkshire. (Habitat type 3.)

Photo V. Todd

Photo 4. *Pteridium aquilinum* and *Anemone nemorosa* in open mixed deciduous woodland, on sand-clay colluvium, Wytham Woods, Berkshire. (Habitat type 7.)

habitat are not equivalent to one another; the numbers from each component are comparable with their counterpart in another habitat.

(2) *Measurement of physical factors*

Ground and air temperatures were taken in the field, and the relative humidity at different levels was measured. This was determined by use of the whirling hygrometer at field-layer or shoulder level, and by Solomon's (1945) method of exposing cobalt thiocyanate paper for measuring humidities on the ground, in cracks of bark or among the leafy branches. This method first entails the preparation of a set of standards, obtained by exposing papers over caustic potash solutions of known density (and humidity). These standards are mounted in liquid paraffin

Table 2. *Seasonal development*

Species	Jan.	Feb.	Mar.	Apr.	May	June
Trogulus tricarinatus	○ . .	No sampling between		. . ○	. . .	○ . .
	. . .	23 Jan. and 22 Mar.		. . .	. ⊙ ⊙	. . .
Anelasmocephalus cambridgei	. . .	. . .	. . .	. . .	. . .	. . .
	. . .		.	⊙ . .	⊙ . ⊙	⊙ ⊙ ⊙
Nemastoma lugubre	. . .		.	. ○ ○	○ ○ ○	○ ○ ○
	⊙ ⊙ ⊙		⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙
N. chrysomelas	. . .		.	. . .	. . .	. . .
Homalenotus quadridentatus	. . .		.	. . .	. . .	. . ○
	. . .		.	. . .	. . .	⊙ . ⊙
Leiobunum rotundum	. . .		.	. ○ ○	○ ○ ○	○ ○ ○
L. blackwalli	. . .		.	. . .	. . ○	○ ○ ○
Mitopus morio	. . .		.	○ ○ ○	○ ○ ○	○ ○ ○
Oligolophus tridens	. . .		.	. . .	○ ○ ○	○ ○ ○
O. agrestis	⊙ ⊙ .		.	. . .	. . ○	○ ○ ○
O. hanseni	. . .		.	. . .	. . ○	○ ○ ○
O. meadei	. . .		.	. . .	. . .	. . .
Odiellus palpinalis	. . .		.	. . .	. ○ ○	○ ○ ○
O. spinosus	. . .		.	. . .	. . .	○ . .
Lacinius ephippiatus	. . .		.	. ○ ○	○ ○ ○	○ ○ ⊙
Phalangium opilio	. . .		.	. . .	. ○ ○	. . .
Opilio parietinus	. . .		.	. . .	. . .	. . .
O. saxatilis	. . .		.	. . .	. . .	. . .
Platybunus triangularis	○ ○ ○		○	○ ○ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙
Megabunus diadema	. ○ ○		○	○ ○ ○	⊙ ⊙ ⊙	⊙ ⊙ ⊙

Species	July	Aug.	Sept.	Oct.	Nov.	Dec.
Trogulus tricarinatus	. . ○	. . .	. . .	. . .	. . .	. . .
	. . .	. . .	. . .	⊙ . .	. . .	. . .
Anelasmocephalus cambridgei	. . ○	○ ○ ○	○ . .	. ○ .	. . ○	. . .
	⊙ ⊙ ⊙	⊙ ⊙ ⊙	. ⊙ .	⊙ ⊙ ⊙	⊙ . .	. . .
Nemastoma lugubre	○ ○ .	. . .	. . .	. . .	. . .	. . .
	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙
N. chrysomelas	. . ○	. . .	. . .	. . .	⊙ . .	. . .
Homalenotus quadridentatus	. . .	. . .	. . .	. . .	. . .	. . .
	. . ⊙	. . ⊙	. . .	. . .	. . .	. . .
Leiobunum rotundum	○ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ .	. . .
L. blackwalli	○ ○ ○	○ ○ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	. . .
Mitopus morio	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ . .	⊙ . .	. . .
Oligolophus tridens	○ ○ ○	○ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	. . .
O. agrestis	○ ○ ○	○ ○ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙
O. hanseni	○ ○ ○	○ ○ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙
O. meadei	. . ○	. . .	. . .	. . .	. . .	. . .
Odiellus palpinalis	○ ○ ○	○ ○ ○	○ ○ ⊙	⊙ . ⊙	⊙ . ⊙	. . .
O. spinosus	. ○ .	. ○ .	. . ⊙	⊙ ⊙ ⊙	. . .	⊙ . .
Lacinius ephippiatus	⊙ ⊙ ⊙	. . .	. . .	. . .	. . .	. . .
Phalangium opilio	○ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ . .	⊙ . .	. . .
Opilio parietinus	○ ⊙ ⊙	⊙ ⊙ ⊙	⊙ ⊙ ⊙	⊙ . .	⊙ . .	. . .
O. saxatilis	. . .	. . ○	⊙ ⊙ .	. . .	. . .	. . .
Platybunus triangularis	⊙ . .	. ○ ○	○ ○ ○	○ ○ ○	○ ○ ○	○ ○ ○
Megabunus diadema	⊙ ⊙ .	. . .	. . .	. . .	. ○ ○	. . .

(○, immature. ⊙, mature.)

between white tiles and clear glass and need be renewed only every 6 months or so. In the field the sensitive paper was suspended inside a piece of glass tubing and left for 2 hr. It was then rapidly transferred to liquid paraffin and later mounted for comparison with the standards. In this way relative humidities between 50 and 100% can be calculated to within 2–3%.

(*d*) *Data from sampling*

(1) *Habitat and seasonal distribution*

Table 1 gives all the British species and indicates whether or not they have been found in the habitats sampled regularly in Wytham Woods, in a cornfield (habitat 15) on the Wytham estate which was visited a few times in the summer, and in Oxford gardens (habitat 16). A key for the determination of British species may be found in Todd (1948).

Nelima silvatica is the only species which was not found in the district during this survey. The species *Trogulus tricarinatus*, *Nemastoma chrysomelas*, *Homalenotus quadridentatus* and *Oligolophus meadei*, that are confined to one or two Wytham habitats are unfortunately all rare species, and therefore of no practical use as indicators of their particular habitats. The commonest woodland species, *Nemastoma lugubre*, *Oligolophus tridens* and *Leiobunum rotundum*, are fairly generally distributed throughout the habitats.

The seasonal development of the species is shown in Table 2. The table is compiled from the Wytham sampling data and from casual records in the case of the garden species. A break in the distribution of the winter species in February and March is due to the absence of sampling at this time. Each month is divided into three periods (1st to 10th, 11th to 20th, 21st to 30th or 31st day) for recording the presence of the species.

Where the records are complete enough it is seen that there are three types of life history found among the harvestmen. There may be survival for the whole year with an overlap of the two generations as in *Nemastoma lugubre* and probably also in *Anelasmocephalus cambridgei*. Or the species (e.g. *Platybunus triangularis* and *Megabunus diadema*) may overwinter in the immature stage, become mature in the spring and early summer and die off before the next generation hatches. Finally, there are the species that mature in the late summer or autumn and spend the winter in the egg stage; this group comprises the majority of the British species.

(2) *Numbers and biomass*

The numbers of harvestmen are not very large, but in deciduous woodland in June there are approximately 50 individuals per square metre of ground litter. The number decreases throughout the year. These are mostly immature specimens, and the maximum biomass is not found until a month later, in July, when there is more than 200 mg. of harvestmen per square metre. The length of the animals was found to have a straight-line relationship with the logarithm of the weight. This was discovered by weighing 5–10 specimens of each of the common species for every 0·5 mm. increase in their length. Using these data a graph was prepared for each species by plotting '*x*' (length) against log '*y*' (weight); a straight line was drawn through the point by eye. From this relationship (see Appendix 1), and knowing, by measurement, the length of each individual, the approximate biomass of any field sample could be calculated.

The numbers of males and females collected appear to be about equal in most of the species, e.g. *Nemastoma lugubre* (123 ♀, 118 ♂); *Oligolophus tridens* (90 ♀, 99 ♂). In *Leiobunum rotundum* the numbers indicate a predominance of males. In the ground and field layers a total of 34 ♀ and 44 ♂ was collected; in the whole habitat (including counts on tree trunks where *L. rotundum* is very abundant) there were 156 ♀ and 381 ♂. The males tend to live longer than the females, which die shortly after egg-laying.

The original sampling records may be found in the Hope Department of Entomology. Table 3 summarizes these records for the commoner species over twelve of the habitats. The sample mean of a species (in heavy black type) is calculated by dividing the sum of the monthly means by the number of months that the species occurs. For although *Nemastoma lugubre* survives the whole year, the majority of species are present for only 6 or 7 months. The maximum monthly mean is also given with the month in which it occurs in brackets after it. The biomass of one square metre quadrat (calculated in the same way as the sample mean) is also given in the table.

This table indicates the stratification of species in the habitats, particularly in woodland. *Anelasmocephalus cambridgei*, *Nemastoma lugubre*, *Odiellus palpinalis* and *Lacinius ephippiatus* are seldom or never found out of the ground layer; *Oligolophus tridens* is not found above the field layer. Table 4 further illustrates this stratification in deciduous woodland. After hatching *Leiobunum rotundum* soon migrates to the field layer and is numerically dominant there in its immature stage. Most *Oligolophus tridens* also move up into the field layer, and are left there as dominant when *Leiobunum rotundum* migrates farther upwards on to the tree trunks from the end of June onwards. Once these two species have left the ground *Nemastoma lugubre* remains as the most abundant form until the following spring.

The frequency or 'constancy' (number of times that the species was found in a total vertical range of

Table 3. *Numbers and biomass*

(N, the upper figure (in heavy type) is the monthly mean count divided by the number of months in which the species was present. The mean count recorded: followed by the month in brackets. B, the mean monthly biomass (weight in mg.) per squa

Habitat	Plant layer	*Anelasmocephalus cambridgei* N.	B.	*Nemastoma lugubre* N.	B.	*Leiobunum rotundum* N.	B.	*L. blackwalli* N.	B.	*Mitopus morio* N.	B.	*Oligolophus tridens* N.	B.
1. Marsh (*Equisetum*)	Gr	**0·00**		**1·00** 4 (8)	2·82	**0·00**		**1·00** 4 (9)	21·68	**0·50** 2 (9)	20·30	**0·50** 1 (5, 8)	3·23
	FL	**0·00**		**0·00**		**0·66** 2 (10)		**0·80** 2 (8, 9)		**0·50** 1 (5, 6, 9)		**0·33** 2 (9)	
2. Marsh (*Carex*)	Gr	**0·00**		**1·90** 10 (6)	4·14	**3·86** 11 (6)	51·11	**3·17** 8 (7)	22·87	**2·14** 4 (6)	65·80	**2·86** 5 (7–9)	26·99
	FL	**0·00**		**0·00**		**0·43** 2 (9)		**1·17** 5 (9)		**0·29** 2 (7)		**0·00**	
3. Mixed decid. wood (SCC)	Gr	**0·09** 1 (10)	0·38	**2·91** 19 (7)	1·91	**3·71** 11 (6)	9·74	**1·17** 3 (6)	1·67	**1·29** 4 (7)	19·29	**4·71** 12 (6)	16·20
	FL	**0·00**		**0·00**		**13·14** 77 (7)		**1·17** 4 (8)		**1·86** 4 (9)		**2·14** 8 (9)	
	Tr	**0·00**		**0·00**		**8·14** 16 (9)		**2·00** 7 (8)		**0·57** 2 (7)		**0·00**	
	Br	**0·00**		**0·00**		**0·43** 2 (8)		**0·00**		**0·14** 1 (10)		**0·00**	
4. Mixed decid. wood (CRL)	Gr	**0·46** 2 (8)	1·34	**4·91** 22 (6)	10·67	**2·57** 7 (5)	13·93	**1·17** 2 (6, 8)	4·70	**1·86** 7 (6)	31·30	**7·71** 12 (6)	42·77
	FL	**0·00**		**0·00**		**9·57** 33 (6)		**1·17** 2 (9, 10)		**4·57** 13 (6)		**6·00** 28 (9)	
	Tr	**0·00**		**0·00**		**18·29** 36 (6)		**1·67** 3 (8, 10)		**1·86** 4 (6)		**0·00**	
	Br	**0·00**		**0·00**		**0·71** 3 (6)		**0·17** 1 (9)		**0·00**		**0·00**	
5. Cut-over decid. wood (SCC)	Gr	**0·22** 1 (5, 6)	0·33	**1·56** 10 (6)	2·76	**1·00** 5 (7)	4·17	**0·20** 1 (6)	0·08	**2·50** 7 (6)	43·47	**6·33** 22 (7)	21·58
	FL	**0·00**		**0·00**		**1·50** 5 (7)		**0·00**		**0·67** 3 (6)		**1·17** 6 (9)	
	Tr	**0·00**		**0·00**		**11·83** 23 (7)		**0·20** 1 (7)		**0·33** 1 (5, 9)		**0·00**	
	Br	**0·00**		**0·00**		**0·00**		**0·00**		**0·00**		**0·00**	
6. Cut-over decid. wood (CRL)	Gr	**0·27** 3 (8)	0·76	**3·82** 14 (5)	7·72	**3·43** 8 (6)	22·13	**0·50** 2 (6)	0·20	**1·86** 7 (6)	13·26	**9·57** 22 (8)	63·26
	FL	**0·00**		**0·00**		**1·43** 2 (6, 7, 8, 10)		**0·50** 3 (10)		**2·57** 10 (6)		**0·14** 1 (8)	
	Tr	**0·00**		**0·00**		**17·43** 41 (8)		**0·83** 2 (9)		**0·71** 3 (7)		**0·00**	
	Br	**0·00**		**0·00**		**0·14** 1 (9)		**0·00**		**0·00**		**0·00**	
7. Bracken (SCC)	Gr	**0·40** 1 (6–9)	1·02	**4·70** 24 (6)	7·81	**0·57** 2 (7)	9·27	**1·33** 4 (10)	7·52	**0·29** 2 (10)	12·27	**3·14** 15 (6)	8·03
	FL	**0·00**		**0·00**		**0·14** 1 (7)		**0·67** 4 (9)		**0·00**		**0·00**	
8. Bracken (CRL)	Gr	**0·30** 1 (5, 7)	0·74	**3·80** 10 (5)	8·18	**2·14** 8 (5)	22·11	**1·00** 5 (8)	19·43	**0·43** 3 (5)	1·59	**2·14** 6 (9)	21·97
	FL	**0·00**		**0·00**		**0·00**		**0·33** 1 (8, 9)		**0·29** 1 (5, 9)		**0·29** 2 (9)	
11. Beech wood	Gr	**0·19** 1 (10)	0·40	**0·67** 2 (5, 6, 11)	1·11	**0·00**		**0·00**		**0·17** 1 (5)	0·17	**0·33** 1 (5, 6)	0·13
12. Conifer wood	Gr	**0·01** 1 (6)	0·10	**0·20** 2 (6)	0·26	**0·71** 5 (6)	1·36	**0·17** 1 (6)	0·03	**0·14** 1 (6)	0·40	**0·57** 2 (6)	0·83
	FL	**0·00**		**0·00**		**1·00** 3 (6)		**1·50** 4 (7)		**0·71** 2 (8)		**0·43** 2 (9)	
	Tr	**0·00**		**0·00**		**5·43** 32 (6)		**0·17** 1 (9)		**0·14** 1 (7)		**0·00**	
	Br	**0·00**		**0·00**		**2·00** 8 (6)		**0·00**		**0·00**		**0·00**	
13. Grassland (SCC)	Gr	**1·18** 6 (6)	2·90	**5·73** 21 (6)	15·46	**0·14** 1 (8)	4·60	**0·00**		**0·14** 1 (7)	8·47	**4·29** 14 (9)	35·20
	FL	**0·00**		**0·00**		**0·29** 2 (8)		**0·17** 1 (8)		**0·00**		**0·00**	
14. Grassland (CRL)	Gr	**0·40** 2 (7)	0·54	**6·30** 37 (10)	19·72	**0·00**		**0·00**		**0·00**		**0·43** 2 (6)	1·70
	FL	**0·00**		**0·00**		**0·00**		**0·17** 1 (7)		**0·00**		**0·00**	

habitat expressed as a percentage of the number of times the habitat was sampled) of a species in the different habitats is given in Table 5. Again the life span of any species has been taken into consideration when calculating its frequency and only those samples taken during this life span comprise the total number of samples counted for that species.

To introduce time and seasonal distribution factors, tables showing the numerical distribution of all the species over the year in any layer of a habitat may be constructed from the sampling data. Table 6 gives the mean monthly numerical and biomass distribution of the species in a square metre litter from the major habitat, deciduous woodland (consisting of the mean of individual samples from deciduous wood (SCC and CRL) and cut-over deciduous wood (SCC and CRL)).

Table 4. *Stratification in woodland*

(Total numbers from 25 samples from oak-ash-sycamore wood (CRL).)

	Sample						
	1 sq.m. litter (day sample)						
Species	A (surface)	B (in moss litter)	C (beneath litter)	$\frac{B+C}{2}$	Sweeping field layer	Count on tree trunks	Beating branches
Anelasmocephalus cambridgei	0	9	1	5	0	1	0
Nemastoma lugubre	0	**46**	**67**	**57**	0	0	0
Leiobunum rotundum	23	4	17	11	**128** (96 imm.)	**278**	8
L. blackwalli	11	0	3	2	14	21	2
Mitopus morio	21	2	14	8	59	26	0
Oligolophus tridens	18	17	**88** (82 imm.)	**53** (49 imm.)	**85**	3	1
O. agrestis	2	6	6	6	7	2	9
O. hanseni	1	1	1	1	2	5	**14**
Odiellus palpinalis	2	13	23	18	2	1	0
Lacinius ephippiatus	2	3	11	7	0	5	0
Platybunus triangularis	2	10	6	8	26	8	0
Megabunus diadema	0	0	0	0	0	18	0

Table 5. *Frequency* (*constancy*)

	Habitats											
	1	2	3, 4	5, 6	7	8	9	10	11	12	13	14
Species	Marsh (*Equisetum*)	Marsh (*Carex*)	Decid. wood (SCC+CRL)	Cut-over wood (SCC+CRL)	Bracken (SCC)	Bracken (CRL)	Shrub woodland	Hawthorn hedge	Beech wood	Conifer wood	Grassland (SCC)	Grassland (CRL)
Trogulus tricarinatus	0	0	0	0	20	9	0	0	0	0	0	17
Anelasmocephalus cambridgei	0	0	20	13	40	27	36	36	10	8	33	25
Homalenotus quadridentatus	0	0	0	0	0	0	0	0	0	0	0	40
Nemastoma lugubre	50	55	70	47	80	91	64	55	40	8	50	67
N. chrysomelas	0	33?	0	0	0	0	0	0	0	0	0	0
Leiobunum rotundum	50	86	97	100	50	86	75	100	67	89	14	0
L. blackwalli	40	100	71	49	67	50	57	83	0	63	17	14
Mitopus morio	43	75	80	75	14	38	50	0	14	50	13	0
Oligolophus tridens	43	63	91	77	43	50	25	63	43	50	75	22
O. agrestis	0	44	65	52	38	50	13	89	13	73	0	22
O. hanseni	0	0	35	36	0	13	11	11	0	18	0	0
Odiellus palpinalis	14	50	60	45	14	50	25	25	0	10	13	11
Lacinius ephippiatus	25	20	64	77	25	20	50	60	0	14	40	17
Platybunus triangularis	11	22	50	72	50	56	33	67	13	50	10	30
Megabunus diadema	0	0	44	63	0	0	43	0	0	38	0	0

Table 6. *Monthly mean numbers from ground-layer samples in mixed deciduous wood (wood (SCC and CRL) and cut-over wood (SCC and CRL)) (May 1946–April 1947)*

Species	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
						Numbers (per sq.m.)						
Anelasmocephalus cambridgei	0	0	0	1	0	1	0	0	0	.	0	0
Nemastoma lugubre	6	11	11	3	1	1	1	1	1	.	0	1
Leiobunum rotundum	5	8	7	1	0	0	0	0	0	.	0	0
L. blackwalli	0	2	1	1	0	1	0	0	0	.	0	0
Mitopus morio	4	5	3	1	0	0	0	0	0	.	0	1
Oligolophus tridens	6	11	12	9	4	3	1	0	0	.	0	0
O. agrestis	1	2	1	1	1	0	1	0	0	.	0	0
Odiellus palpinalis	1	4	2	3	1	2	0	0	0	.	0	0
Lacinius ephippiatus	5	5	1	0	0	0	0	0	0	.	0	1
Platybunus triangularis	1	1	1	2	3	4	1	1	0	.	0	0
Total	29	49	39	22	10	12	4	2	1	.	0	2
						Biomass (mg.)						
Anelasmocephalus cambridgei	0·0	0·0	0·0	2·7	0·0	1·8	0·0	0·0	0·0	.	0·0	0·0
Nemastoma lugubre	5·1	13·8	26·5	9·9	4·0	4·0	3·5	2·9	3·4	.	0·0	0·8
Leiobunum rotundum	3·8	11·4	37·6	21·1	0·0	0·0	0·0	0·0	0·0	.	0·0	0·0
L. blackwalli	0·0	0·9	1·8	2·0	0·0	7·2	0·0	0·0	0·0	.	0·0	0·0
Mitopus morio	14·3	56·9	75·8	18·7	0·0	0·0	0·0	0·0	0·0	.	0·0	0·7
Oligolophus tridens	3·3	9·3	36·4	65·6	70·5	47·9	16·4	0·0	0·0	.	0·0	0·0
O. agrestis	0·4	0·5	1·8	4·7	7·7	8·8	7·8	0·0	0·0	.	0·0	0·0
Odiellus palpinalis	0·5	3·3	2·7	13·1	7·1	14·6	0·0	0·0	0·0	.	0·0	0·0
Lacinius ephippiatus	17·6	38·0	16·0	0·0	0·0	0·0	0·0	0·0	0·0	.	0·0	0·4
Platybunus triangularis	42·8	41·6	14·6	0·2	1·6	3·7	2·4	0·4	0·0	.	0·0	0·0
Total	87·8	175·7	213·2	138·0	90·9	88·0	30·1	3·3	3·4	.	0·0	1·9

This shows any seasonal peaks in the numbers, though these are rather small; the highest number is found when the species is immature. In a litter species, e.g. *Nemastoma lugubre* or *Lacinius ephippiatus*, the subsequent fall in number is probably associated with mortality, but in a species like *Leiobunum rotundum*, which undergoes a vertical migration the fall in number is partly due to this movement upwards. The species totals for each month give an estimate of the number and weight of individuals to be found in a square-metre litter at any time of the year. When the biomass is considered *Mitopus morio* and *Platybunus triangularis*, which are never very abundant, become more important owing to their large adult size.

By converting abundance figures to 'dominance' ones it is possible to obtain relative values for the numbers of species in any habitat layer or habitat. Dominance, however, gives no indication of abundance and may be very misleading, e.g. *Nemastoma lugubre* has a mean density of 4·91 individuals per square metre sample in deciduous woodland and 0·67 as the corresponding number in beech wood. Expressed as dominance

$$\left(\frac{\text{Mean number per sample for species}}{\text{Sum mean numbers per sample for all species}}\%\right)$$

it is 20·1 % dominant in woodland and 41·1 % dominant in beech litter. The temporal relations of the various species are a further complication which would need to be considered in such a conversion. For these reasons no comparisons of population in the different habitats have been undertaken, and also for the more practical reason that the same number of vertical layers do not exist in all the habitats.

It is believed that an intimate acquaintance with the habits of the species, a knowledge of their life histories, their seasonal development and their habitat distribution are of more use in the determination of harvestmen populations than any techniques of capturing or counting so far met with.

(3) *The vertical migration of some woodland species in relation to time*

Mention has already been made of the upward migration of *Leiobunum rotundum* and *Oligolophus tridens*. Many other species show a vertical migration during their life histories and this movement is illustrated in Figs. 1–4.

Structurally *Leiobunum rotundum* and *L. blackwalli* resemble each other very closely, but it is seen that during their life histories there is no habitat overlap in

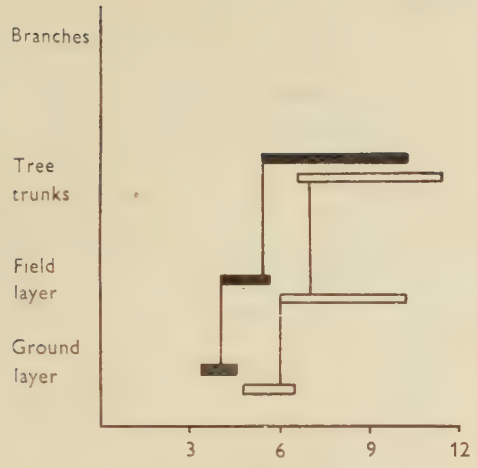

Fig. 1.

Leiobunum rotundum.
Leiobunum blackwalli.

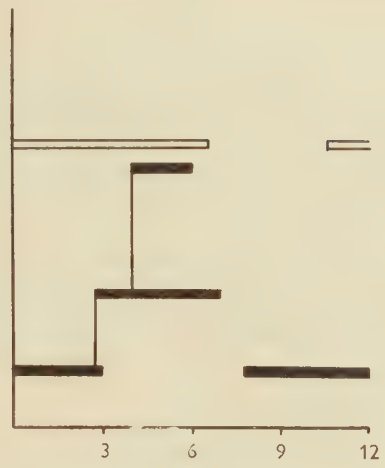

Fig. 2.

Platybunus triangularis.
Megabunus diadema.

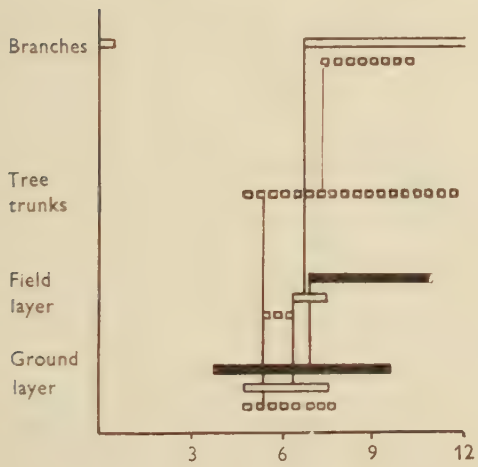

Fig. 3.

Oligolophus tridens.
Oligolophus agrestis.
Oligolophus hanseni.

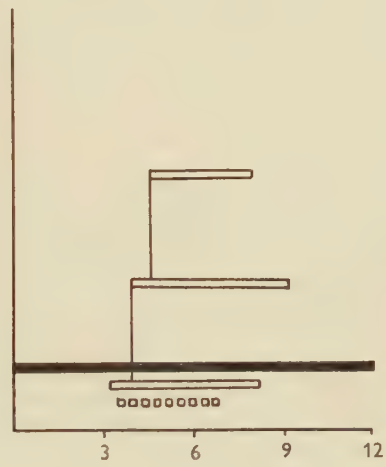

Fig. 4.

Nemastoma lugubre
Mitopus morio.
Lacinius ephippiatus.

Figs. 1–4. Spatial and temporal relations of some woodland species.

time until they both appear on the tree trunks (Fig. 1). *L. rotundum* hatches about a month in advance of *L. blackwalli* and it retains this lead as it ascends from one plant layer to the next. *L. blackwalli* is never abundant and it is usually found on the lower parts of the tree trunks. *L. rotundum* is very abundant and is found from the base to 7 ft. up the trunks. It should be noted that the figures are diagrammatic; in all the species the females must eventually come on to the ground to lay their eggs, though it is possible that *Megabunus diadema* lays its eggs on the bases of trees, as no *M. diadema* have been taken on the ground. The habitat relation of this species is shown with that of *Platybunus triangularis*, another over-wintering form (Fig. 2).

The relations of the three *Oligolophus* spp. are shown in Fig. 3. *O. tridens*, which is a dominant field-layer form, is the only numerically important species.

O. hanseni is found predominantly on the tree trunks and also among the branches, where it occurs with the third species, *O. agrestis*. Fig. 4 shows the habitat relations of *Mitopus morio*, *Nemastoma lugubre* and *Lacinius ephippiatus*. The first is a predator on other harvestmen on the field layer, *Nemastoma lugubre* is confined to the ground for the whole year and *Lacinius ephippiatus*, with its short life-span, also keeps to the ground layer.

Vertical migration during the life history results in the spatial separation of the closely allied *Leiobunum* spp., and to a less extent species of the genus *Oligolophus*. This separation has possibly been significant in the evolution of these species.

(*e*) *Night transects*

In 1927, nocturnal ecology was described by Allee as an almost unexplored field of research. Since this time a great deal of pioneer work has been done by O. Park and his associates (1931, 1935, 1936) on the movements and rhythms of nocturnal invertebrates and the methods of recording these. Harvestmen, collected during the regular daytime sampling, were usually in a quiescent state, although *Leiobunum* spp. were sometimes seen running over the ground or tree trunks. Of course it is difficult to prove that these were not disturbed individuals. Certainly, at night all the species showed an increased activity which was associated with feeding.

A series of six parallel trails, about 5 yards apart and 30 yards long, was marked out in mixed deciduous woodland (CRL). In each of these, ten trees were numbered (sixty trees altogether). The six trails were worked over in order by torchlight every 2 hr. from an hour or so before dusk until after dawn on 19 July, 12, 13 and 17 August 1947. Harvestmen that were active on the field layer (a yard either side of the trail) and on the marked trees were noted. Measurements of ground and air temperatures, and the percentage relative humidity at field-layer level were taken each time before beginning the third trail.

The numbers and activity of *L. rotundum* (easily distinguished in the field at this stage from the immature *L. blackwalli*) and *Mitopus morio* were noted. Also present at the time of the first census was a third species, *Lacinius ephippiatus*, which had practically disappeared a month later. Litter species such as *Nemastoma lugubre* and immature *Odiellus palpinalis* were found to be active at night on the ground, which layer was not included in the censuses. Table 7 shows the number of the three species observed at the different times of counting on the four occasions.

The greatest number of active *Mitopus morio* and *Lacinius ephippiatus* was observed between the hours 9 p.m. and 1 a.m. (G.M.T.) *Mitopus morio* was seen most frequently walking over the surface of *Mercurialis perennis* which forms the field layer, though a few animals, nearly all males, ascended the tree trunks. *Lacinius ephippiatus* was also seen on the upper surface of *Mercurialis* leaves. In all the transects the number of active *Leiobunum rotundum* observed begins to decrease from about 9 p.m. and the number of active animals never approaches the total number (including inactive ones) seen. The total numbers seen on tree trunks show that practically all *L. rotundum* leave the trees for the field layer at dusk and return there at dawn. Now nearly all *L. rotundum* observed on the field layer between these hours were eating other animals. Further, it was discovered that many *L. rotundum* were hidden from sight as they made their way along the under side of the *Mercurialis* leaves. It is here, presumably, that these harvestmen hunt for food, and on the upper surface of the leaves that they bring the prey to devour it. This habit of hunting on the under surface of the leaves will explain the small number of active *Leiobunum rotundum* observed during the counts.

The activity of the animals appears to be associated with the increase in the percentage relative humidity and the decrease in temperature in the wood during the night. The activity begins with the approach of dusk and declines at the onset of dawn.

From a study of the daytime sampling data *L. rotundum* was regarded as a dominant tree-trunk form. This nocturnal feeding activity on the field layer, involving a nightly inter-stratal migration, was quite unexpected. The prey captured by *L. rotundum* and *Mitopus morio* in the field layer at night showed great diversity. In America, O'Brien (1947) has reported that harvestmen occupy a predator niche in the food network of a forest community in the Chicago area; the same might be said of these species in Wytham Woods.

Copulation in *Leiobunum rotundum* was observed on three occasions during these transects. It took place on the tree trunks before dusk between 5 and 5.30 p.m. *Lacinius ephippiatus* was consistently found in litter in the daytime sampling. It also appears to migrate to the field layer to feed at night.

3. LABORATORY INVESTIGATIONS

In the laboratory, harvestmen were kept in various glass containers, the bottoms of which were covered with plaster of Paris that was kept damp. The containers were placed in an incubator at $16{\cdot}5 \pm 0{\cdot}2°$ C. The air in the incubator was circulated by a small fan (driven by a motor outside the incubator); an electric heating coil, placed directly in front of the fan, raised the air to the required temperature which was controlled by a Sunvic thermostat. To obtain this temperature ($16{\cdot}5°$ C.) in the summer, water cooled by refrigeration to approximately 10° C. was circulated in a closed circuit from a refrigerating tank (outside

Table 7. *Numerical and climatic data from night transects*

Species	G.M.T. 3 p.m.	5 p.m.	7 p.m.	9 p.m.	11 p.m.	1 a.m.	3 a.m.	5 a.m.	7 a.m.	9 a.m.
					19 July					
FL and Tr:										
Leiobunum rotundum	.	4	26	7	18	19	36	38	.	.
L. rotundum (active and inactive)	.	43	66	16	26	19	36	38	.	.
Mitopus morio	.	4	5	50	66	42	18	7	.	.
Lacinius ephippiatus	.	0	0	18	41	21	12	0	.	.
Tr only:										
Leiobunum rotundum (active and inactive)	.	40	48	3	4	1	28	38	.	.
Mitopus morio	.	3	3	11	12	6	3	5	.	.
M. morio (males only)	.	2	2	10	11	6	2	5	.	.
FL level:										
R.H. (%)	.	.	81	88	89	90	89	85	.	.
Air temp. (° C.)	.	18·5	17·0	15·0	14·5	14·0	13·5	13·0	.	.
Ground temp. (° C.)	.	18·0	15·5	15·5	15·0	14·5	14·0	13·5	.	.
					12 August					
FL and Tr:										
Leiobunum rotundum	.	.	21	40	37	21	21	12		.
Mitopus morio	.	.	3	35	25	22	22	2	.	.
Lacinius ephippiatus	.	.	0	0	0	0	2	1	.	.
FL level:										
R.H. (%)	.	.	.	74	77	84	86	89	.	.
Air temp. (° C. at 4 ft.)	.	.	20·5	18·0	17·0	14 5	13·0	12·5	.	.
Ground temp. (° C.)	.	.	18·0	16·5	16·0	15·0	14·0	13·5	.	.
					13 August					
FL and Tr:										
Leiobunum rotundum	2	8	26	48	38	40	30	16	10	1
L. rotundum (active and inactive)	68	37	26	48	38	40	30	16	25	37
Mitopus morio	0	0	2	43	43	33	19	3	0	0
FL level:										
R.H. (%)	.	60	75	82	84	87	88	89	.	.
Air temp. (° C.)	.	24·5	21·0	18·5	17·0	14·5	13·5	12·5	.	.
Ground temp. (° C.)	.	21·0	18·5	17·5	16·5	15·0	14·0	13·0	.	.
					17 August					
FL and Tr:										
Leiobunum rotundum	.	14	24	34	32	15	17	10	.	.
Mitopus morio	.	0	1	43	39	37	20	2	.	.
FL level:										
R.H. (%)	.	69	76	76	78	83	90	Rain	.	.
Air temp. (° C. at 4 ft.)	.	25·0	24·0	22·0	20·0	18·0	17·0	.	.	.
Ground temp. (° C.)	.	21·5	20·5	19·5	19·0	17·5	17·0	.	.	.

the incubator and installed by Pressed Steel Co. Ltd., Oxford), into a coil at one end of the incubator and back to the tank. The temperature was then raised by the heater which was controlled by the Sunvic thermo-regulating device.

All the woodland harvestmen were kept in the laboratory at R.H. between 85 and 100% saturation. This was maintained by damping the plaster base of the containers, placing in each a small tube full of water and covering the top with a glass plate. A

muslin covering replaced the glass when keeping garden or grassland species in the laboratory. As high humidities favoured the growth of moulds the plaster bases were wiped over with very dilute copper sulphate solution once a week.

A mixture of dried egg, wholemeal flour and yeast ('Aluzyme', Phillips Yeast Products Ltd.) was used as a basic laboratory food. This had the disadvantage that when placed in a saturated atmosphere it gradually absorbed water, so that the food had to be changed daily. Live animal food, in the form of psocids (*Liposcelis granicola* Broadhead & Hobby), and larvae of *Tribolium confusum* Duval, both of which were cultured in the laboratory, supplemented the diet. Water for drinking was supplied as part of the humidity arrangements.

Under these conditions of temperature, humidity and food, most of the species developed to maturity, mated and laid eggs.

(*a*) *Reactions to humidity*

(1) *Humidity preference*

Experiments were carried out in a dark cellar at a temperature between 15·5 and 17·5° C. The size and activity of harvestmen determined the form of apparatus. The experimental chamber was a rectangular aquarium, 24 in. long by 8 in. wide by 4 in. deep. This was enclosed in an insulated Tentex box, the lid of which had a transparent celluloid window which allowed the temperature to be read on a thermometer inside, without the lid being opened. A humidity gradient was obtained by placing a container with water at one end of the chamber and one with sulphuric acid at the other (200 c.c. distilled water and 150 c.c. of 60% sulphuric acid were used). A tray of copper gauze, covered with fine muslin (to provide a suitable surface for the animals to walk on) was placed over and just above these dishes; leaving $2\frac{1}{2}$ in. between the gauze and the rim of the aquarium. The whole aquarium was covered with a glass plate, sealed with vaseline and then left for 48 hr. to get into equilibrium. In this way a straight-line diffusion gradient of humidity from 35 to 90% R.H. was obtained. The whole length of the gradient was calibrated between these values. The main calibrations (at 3 in. intervals) were determined by direct measurement, using cobalt thiocyanate papers (Solomon, 1945), and the intermediate ones by interpolation.

Once established, the gradient remained fairly stationary for 2 or 3 weeks; before each experiment it was checked and corrected if necessary. The calibration of the gradient made it possible, during an experiment, to assign a definite number to each individual at any time of observation. Eight (where possible four males and four females) marked individuals of a species were introduced into the chamber in each experiment, and their position along the gradient noted every 20 min. over a period of 80 min. Thus there were four records for each individual in every experiment. The same animals were tested twice in one day and on the second occasion they were introduced at the opposite end of the gradient from the previous time. The whole experiment was then repeated on another day with eight new individuals of the same species. In this way 128 observations were obtained for each species. The animals were marked with different colours of 'Joy' cellulose brushing enamel, which dries very quickly.

The four species *Nemastoma lugubre* (litter), *Oligolophus tridens* (ground and field layer), *Leiobunum rotundum* (field layer and tree trunk) and *Odiellus spinosus* (garden) were tested in this way. The detailed results are deposited in the Hope Department of Entomology, University Museum, Oxford; a statistical analysis of these results is presented in Appendix 2*a*. Here it is shown that there is a significant difference between the preferences of the species. $F_{(3,63)}=9{\cdot}1 \quad P<0{\cdot}001$.

In a similar experiment *Anelasmocephalus cambridgei* (grassland and litter), *Leiobunum blackwalli* (field layer and tree trunks), *Oligolophus agrestis* (field layer and branches) and *O. hanseni* (tree trunks and branches) were tested; again there was found to be a significant difference between the humidity preferences of the species. $F_{(3,63)}=14{\cdot}7 \quad P<0{\cdot}001$. (Appendix 2*b*).

The fiducial limits ($t_{0{\cdot}05[31]}=2{\cdot}042$) of humidity preference for all the species have been calculated (Appendix 2*a*), and are shown diagrammatically in Fig. 5. Combining the results of these two experi-

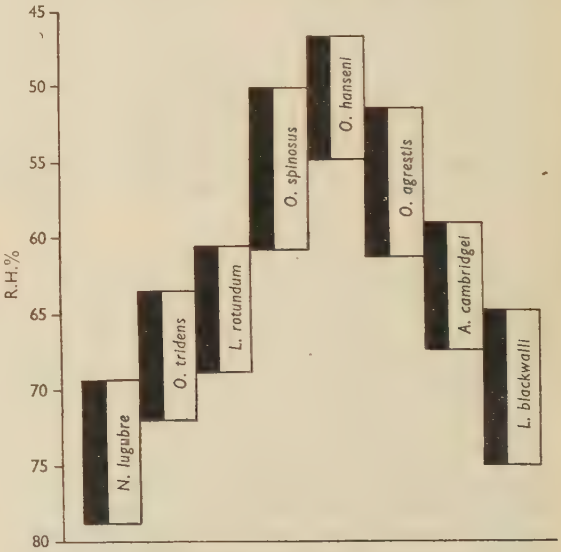

Fig. 5. Fiducial limits of humidity preference $t_{0{\cdot}05[31]}=2{\cdot}042$.

Photo V. Todd

Photo 5 Cut-over oak-ash-sycamore wood, with coppiced sycamore in foreground, on Coral Rag, Wytham Woods, Berkshire. (Habitat type 6.)

Photo V. Todd

Photo 6. *Brachypodium pinnatum* grassland on Coral Rag, Wytham Woods, Berkshire. Metre square quadrat. (Habitat type 14.)

ments the standard error of a difference (=3·16) and therefore the fiducial limits of a difference may be calculated (Appendix 2*c*). *Odiellus spinosus* appears to have a humidity preference significantly different from all the species except *Oligolophus agrestis* and *O. hanseni*. *O. tridens* is significantly different from these two allied species but shows no difference from *Leiobunum rotundum*, *L. blackwalli* or *Anelasmocephalus cambridgei*. *Nemastoma lugubre* (litter species) has a preference significantly different from all the species except *Leiobunum blackwalli*.

No difference in preference between the sexes of any species has been demonstrated.

(2) *Survival at different humidities*

The experiments were carried out in an incubator at 16·5 ± 0·2° C. Desiccators were prepared, using supersaturated solutions of salts to produce a range of humidities. These were 77 % R.H. (sodium chloride), 86 % R.H. (potassium chloride), 94 % R.H. (potassium nitrate) and 100 % R.H. (distilled water); see Adams & Merz (1929). Four small jars, each capable of housing two harvestmen, were introduced into each desiccator. Fine muslin covers were placed over the small jars. In each experiment 32 specimens of the species (where possible 16 males and 16 females) were used. One male and one female were put into each jar so that there were eight animals at each humidity. They were given no food. The jars were examined every 4 hr. (omitting early hours of the morning) and any dead specimens removed and noted.

Three woodland species, *Leiobunum rotundum* (both mature and immature specimens), *Mitopus morio* and *Oligolophus tridens* and the garden species *Odiellus spinosus* were subjected to this treatment. The results, given as hours of survival at the different humidities are shown in Table 8 (complete records are

Table 8. *Survival in hours at* 16·5 ± 0·2° *C.*

Species	R.H. (%) 77	86	94	100	Significance of difference between treatments
Leiobunum rotundum	42·0 ± 4·4	69·9 ± 11·4	86·6 ± 13·9	105·0 ± 13·6	*
Immature *L. rotundum*	55·0 ± 9·9	72·6 ± 14·5	144·8 ± 15·8	179·6 ± 29·7	**
Mitopus morio	58·4 ± 11·3	84·8 ± 18·8	152·5 ± 26·7	191·9 ± 17·2	**
Oligolophus tridens	32·0 ± 4·4	41·0 ± 7·9	61·4 ± 10·1	104·6 ± 10·9	**
Odiellus spinosus	242·5 ± 25·6	260·5 ± 25·6	350·0 ± 34·2	241·4 ± 15·7	N.S.

* Sig. 1·0 %. ** Sig. 0·1 %. N.S. Not significant.

n the Hope Department of Entomology). The signi-icance of the difference (from an analysis of variance) between the treatments is indicated.

In all the woodland species the survival time increases with increasing humidity. In *O. spinosus* there appears to be no significant difference in the survival time at the various humidities. The survival time of this species at any humidity is much longer than that of any of the other species.

(*b*) *Reactions to temperature*

Roedel (1881, p. 24) found the vital minimum temperature for *Phalangium opilio* to be −9° C. After an hour's exposure to this temperature the animals died; after 15 min. exposure they lived for 10 hr.

(1) *Temperature preference*

The apparatus used consisted of two insulated metal chambers (8 in by 9 in. by 10 in. deep) connected by a solid brass trough (26 in. long by 2¼ in. wide by 1 in. deep), which was also insulated. One chamber was filled with a mixture of ice and salt (about 6 : 1) and the other with water which was kept at a constant hot temperature by thermostatic control. In this way a temperature gradient was produced along the brass trough from the cold to the hot end. Fine cotton gauze, stretched over wire provided a false floor to the trough and gave a suitable surface for the animals to walk on. A strip of glass fitted over the trough to close it, and this was covered by two strips of Tentex for insulation purposes. The length of the trough was calibrated in degrees centigrade by placing thermometers along it at 3 in. intervals, plotting the readings and interpolating the intermediate values. The gradient in the first experiments was −4 to 20° C.; in later ones it was from −1 or 4° to 25° C. A 100 % R.H. was maintained along the trough by placing tiny metal dishes full of water below the cotton gauze floor.

As in the humidity preference experiments eight marked animals were introduced into the trough in an experiment, and the position of each individual in relation to the gradient was noted every 15 min. over a 60 min. period (four readings per individual). Up till the time of the experiment the harvestmen were kept in an incubator at 16·5° C.

Eight specimens of *Nemastoma lugubre*, *Anelasmocephalus cambridgei*, *Leiobunum rotundum*, *L. blackwalli*, immature *Platybunus triangularis* and *Odiellus spinosus* were subjected to this preference experiment

Table 9. *Temperature preference* (100% R.H.)

Species	Mean (° C.)	Fiducial limits (° C.)
Platybunus triangularis imm.	8·8	6·5–11·1 ($t_{0.05[15]}=2·131$)
Nemastoma lugubre	9·6	7·3–11·9 ($t_{0.05[15]}=2·131$)
Oligolophus tridens	10·3	8·7–11·9 ($t_{0.05[31]}=2·042$)
Mitopus morio	11·8	10·4–13·2 ($t_{0.05[31]}=2·042$)
Leiobunum blackwalli	12·4	11·1–13·7 ($t_{0.05[15]}=2·131$)
L. rotundum	13·9	11·9–15·9 ($t_{0.05[15]}=2·131$)
L. rotundum	13·9	12·4–15·4 ($t_{0.05[31]}=2·042$)
Phalangium opilio	15·5	13·4–17·6 ($t_{0.05[31]}=2·042$)
Anelasmocephalus cambridgei	16·3	15·0–17·6 ($t_{0.05[15]}=2·131$)
Odiellus spinosus	16·3	15·2–17·4 ($t_{0.05[15]}=2·131$)

twice, giving 64 readings for each species. Sixteen *Oligolophus tridens*, *Mitopus morio*, *Phalangium opilio* and further specimens of *Leiobunum rotundum* were tested twice, thus giving 128 readings per species in this series. Recorded results from these experiments are deposited in the Hope Department of Entomology. Table 9 gives the mean preference value calculated for the species and the fiducial limits.

(2) *Heat death-point, and cold tolerance*

Some preliminary experiments indicate that the heat death points of *Platybunus triangularis*, *Leiobunum rotundum*, *Mitopus morio* and *Oligolophus tridens* all lie between 38·2 and 38·5° C. The results are based on survivals counted 10 hr. after an hour's exposure in a saturated atmosphere. The heat death point of *Odiellus spinosus* is higher than this: it is about 42·0° C.

Preliminary experiments show that most of the species will stand an hour's exposure to temperatures as low as −4·0 to −4·5° C., when transferred to this temperature from 16·5° C.

(*c*) *Note on oviposition and development*

In a recent paper Holm (1947) deals with the development of *Opilio parietinus*. He found that this species laid from 20 to 60 eggs at 20° C., and that there was no further development after an early blastoderm stage unless the eggs were transferred to a refrigerator, where they were kept at 6° C. for 2 weeks and then for a further week at −6° C.

Eggs of *Platybunus triangularis*, an overwintering species which normally emerges at the end of the summer, yielded an 80–90% hatch at room temperature at Oxford. A period of cold treatment increased the percentage yield for the eggs of all the species which normally overwinter in the egg stage, except *Leiobunum blackwalli*; the percentage hatch of this species was not significantly higher after cold treatment.

A saturated atmosphere, or one approaching saturation, favoured the emergence of the harvestmen. There appear to be seven ecdyses during the life history of *L. rotundum*, *Platybunus triangularis* and *Phalangium opilio*; these include the casting of the first hairless skin at hatching.

4. CORRELATION OF FIELD AND LABORATORY OBSERVATIONS

(*a*) *Humidity*

The relative humidity at different levels in oak woodland varies very much, depending on the time and type of day. From August to October the relative humidity of the field layer is generally between 70 and 80%, and that of the ground layer between 85 and 100%. Measurements taken in cracks of the bark of oak gave values between 75 and 82%: and on the tree trunks themselves between 60 and 70% R.H. The humidity among branches, on the under surface of leaves, was 60–65%, and this varies with the evaporating power of the air and the amount of transpiration from the leaves. There is seen to be a general gradient of decreasing humidity from the ground layer to the tree-tops. Results from humidity preference experiments in the laboratory show a correlation with the measurements and observations in the field, when the vertical stratification of the species in the wood is considered (see Table 10).

(*b*) *Temperature*

Owing to the blanketing effect of the vegetation the temperature in a wood does not respond quickly to changes in the surrounding air temperature, nor does it ever reach temperatures as high or as low as the air outside it. On the other hand, the temperature in open grassland or a cornfield will correspond much more closely to external air temperatures. Temperature preference experiments suggest that temperature may influence the choice of habitat of a species. Harvestmen such as *Nemastoma lugubre*, *Platybunus triangularis* and *Oligolophus tridens*, which have a low range of temperature preference (up to 11·9° C.), tend to be ground or field-layer species in the woodland. *Nemastoma lugubre*, a dominant litter form, is also abundant in open grassland: here it is found beneath

Table 10. *Correlation between stratification of species in field and their humidity preference as tested in laboratory*

Field R.H. (%)	Plant layers	Species	Fiducial limits of humidity preference $t_{0.05[31]}=2.042$
50–60	Branches	*Oligolophus hanseni*	46·8–54·8
		O. agrestis	51·5–61·3
60–75	Tree trunk	*Leiobunum rotundum*	60·7–68·9
		L. blackwalli	64·9–75·1
70–80	Field layer	*Oligolophus tridens*	63·5–72·1
85–100	Ground layer	*Nemastoma lugubre*	69·4–78·8

the vegetation next to the soil, where it is probably not exposed to such extreme changes of temperature as species living among the stalks of the grass. *Anelasmocephalus cambridgei* is such a species, and it has a temperature preference range between 15·0 and 17·6° C. *Phalangium opilio*, a cornfield species and *Odiellus spinosus* from gardens also have a much higher range of temperature preference than the woodland species.

(*c*) *Egg laying*

The increased percentage yield obtained by exposing the eggs of harvestmen (which normally overwinter in the egg stage) to a period of cold treatment indicates that this overwintering in the field is a very essential part of their life history. *Leiobunum blackwalli* provided an exception to this, and presumably it is only the cold of winter that prevents this species from hatching a few weeks after laying in the field.

The eggs of harvestmen are laid in the ground, under stones, in cracks in wood or on moss-covered bark where the humidity is always high. In the laboratory the highest hatch yield was obtained when the eggs developed at humidities between 94 and 100%.

5. ACKNOWLEDGEMENTS

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6. SUMMARY

1. The twenty-one British species of harvestmen have all been found in the Oxford district with the exception of *Nelima silvatica*. Seventeen of them have been found in Wytham Woods, Berkshire, where the main research was done.

2. There are three main types of life history found among the harvestmen. They may be found all the year round and have an overlap of the generations (e.g. *Nemastoma lugubre*); or they may be annuals which die before their eggs hatch. Of the annuals some hatch in the autumn and overwinter as immature forms (e.g. *Platybunus triangularis* and *Megabunus diadema*); others, including the majority of species, emerge in the spring and die off at the end of the autumn

3. The numbers of harvestmen are never very large. In June, a maximum number of approximately 50 may be found in a square metre ground layer in deciduous woodland. The maximum biomass is found in July when there were more than 200 mg. of harvestmen per square metre in this habitat.

4. There are three main woodland species in Wytham Woods: *Nemastoma lugubre* found on the ground layer, *Oligolophus tridens* on the ground and field layer and *Leiobunum rotundum* on the tree trunks.

5. There is usually microhabitat separation in space and time, or both, of closely allied species of the same genus.

6. Harvestmen are most active at night. This activity is correlated with the decrease in light intensity, increase in relative humidity and decrease in temperature in the wood.

7. *L. rotundum* leaves the tree trunks at night and feeds on the field layer. It hunts on the under surface of *Mercurialis perennis* leaves.

8. There was found to be a strong correlation between the humidity preference of the species as tested in the laboratory and their stratification in oak woodland.

APPENDICES

Appendix 1. *Weight in milligrams*

Species	Length (mm.) 0·5	0·75	1·0	1·25	1·5	1·75	2·0	2·25	2·5	2·75	3·0	3·25	3·5	3·75	4·0	♀	♂
Anelasmocephalus cambridgei	.	.	.	.	1·5	.	2·2	.	3·0	.	.	.	.	.	.	3·6	2·0
Nemastoma lugubre	0·4	0·6	0·8	1·0	1·4	2·0	2·7	3·7	5·0	.	.	.	.	.	.	4·6	2·8
Leiobunum rotundum	0·5	0·7	1·2	1·4	2·0	2·8	4·0	5·5	7·9	10·9	15·5	.	30·2	.	.	32·2	20·8
L. blackwalli	0·4	0·6	0·8	1·2	1·8	2·6	4·0	6·3	10·0	13·8	20·4	.	.	.	3·0 mm. = 18·2 4·0 mm. = 35·0	. 10·1
Mitopus morio	.	.	1·0	1·4	1·9	2·5	3·2	4·2	5·5	7·2	9·6	12·5	15·8	21·3	27·5	59·3	26·6
Oligolophus tridens	0·2	0·5	0·9	1·3	2·0	2·7	3·6	4·8	5·7	7·0	8·7	10·0	11·4	13·4	3·5 mm. = 13·7 4·0 mm. = 26·4	. 10·5
O. agrestis	Calculated as for *O. tridens*, as data here inadequate														3·5 mm. = 14·6 4·0 mm. = 20·9	. 10·1
O. hanseni	Calculated as for *O. tridens*, as data here inadequate															23·0	11·3
Odiellus palpinalis	0·4	0·6	0·9	1·3	1·9	2·6	3·7	5·2	7·8	.	.	.	.	.	.	12·1	7·3
Lacinius ephippiatus	.	.	1·0	1·4	1·8	2·3	2·9	3·7	4·8	6·0	7·8	10·0	12·6	15·9	20·4	33·6	16·6
Platybunus triangularis	0·2	0·5	0·9	1·5	2·1	3·1	4·2	5·4	6·9	8·1	10·2	12·5	14·4	17·3	20·8	43·1	18·5
Megabunus diadema	.	.	.	.	.	.	3·5	.	4·7	.	6·7	.	.	.	.	9·0	7·2

Appendix 2*a*. *Exp.* 1. *Humidity preference.*

Analysis of variance

		Degrees of freedom	Sum of squares	Mean square	*F*
Days (D)		1	644	644	.
Species (S)		3	5728	1909	9·1**
DS		3	94	31	.
Error between animals	*Odiellus spinosus*	14	3300	236	.
	Oligolophus tridens	14	2141	153	.
	Nemastoma lugubre	14	3512	251 = 207·9	.
	Leiobunum rotundum	14	2687	192	.
Total		63	18106	.	.
Ends (E) (of gradient)		1	29	29	.
DE		1	37	37	.
SE		3	666	222	.
DSE		3	111	37	.
Error within animals	*Odiellus spinosus*	14	3184	227	.
	Oligolophus tridens	14	1919	137	.
	Nemastoma lugubre	14	1135	81	.
	Leiobunum rotundum	14	811	58	.
Total		127	25998	.	.

Comparison of four sets of data (*using mean square totals*)

	Degrees of freedom	Sum of squares	Mean square	$s_{\bar{x}}^2$	Standard error	Fiducial range (±) ($t_{0.05[31]} = 2.042$)
Odiellus spinosus	31	6842	220·7	6·897	2·626	5·4
Oligolophus tridens	31	4307	138·9	4·341	2·083	4·3
Nemastoma lugubre	31	5199	167·8	5·244	2·290	4·7
Leiobunum rotundum	31	3920	126·5	3·953	1·988	4·1

Appendix 2*b*. *Exp.* 2. *Humidity preference.*

Analysis of variance

		Degrees of freedom	Sum of squares	Mean square	*F*
Days (D)		1	86	.	.
Species (S)		3	6689	2230	14·7**
DS		3	830	.	.
Error between animals	*Oligolophus agrestis*	14	3567		.
	Anelasmocephalus cambridgei	14	933		
	Leiobunum blackwalli	14	2006	151·9	.
	Oligolophus hanseni	14	2003		.
Total		63	.	.	.
Ends (E)		1	107	.	.
DE		1	96	.	.
SE		3	3013	.	.
DSE		3	408	.	.
Error within animals	*Oligolophus agrestis*	14	1713	.	.
	Anelasmocephalus cambridgei	14	1102	.	.
	Leiobunum blackwalli	14	2599	.	.
	Oligolophus hanseni	14	1164	.	.
Total		127	26312	.	

Appendix 2*b*. (*cont.*)

Comparison of four sets of data (using mean square totals)

	Degrees of freedom	Sum of squares	Mean square	$s_{\bar{x}}^2$	Standard error	Fiducial range (±) ($t_{0.05[31]}=2.042$)
Oligolophus agrestis	31	5622	181·4	5·669	2·381	4·9
Anelasmocephalus cambridgei	31	4001	129·1	4·034	2·009	4·1
Leiobunum blackwalli	31	6255	201·8	6·306	2·511	5·1
Oligolophus hanseni	31	3815	123·1	3·847	1·961	4·0

Appendix 2*c*. *Combining Exps.* 1 *and* 2.

Short analysis of variance

	Degrees of freedom	Sum of squares	Mean square	*F*
Species	7	14277	2039·6	12·8
Times	3	731	.	.
Error	245	39160	159·8	.
Total	255	54168	.	.

Error mean square = 160 (159·8)

S.E. $= \sqrt{\frac{160}{32}} = 2{\cdot}23$

Species means:

Odiellus spinosus	55·5 ± 2·23	*Oligolophus agrestis*	56·4 ± 2·23
Oligolophus tridens	67·8 ± 2·23	*Anelasmocephalus cambridgei*	63·3 ± 2·23
Nemastoma lugubre	74·1 ± 2·23	*Leiobunum blackwalli*	70·0 ± 2·23
Leiobunum rotundum	64·8 ± 2·23	*Oligolophus hanseni*	50·8 ± 2·23

S.E. of a difference $= \sqrt{\left(2 \times \frac{160}{32}\right)} = 3{\cdot}16.$

Therefore the fiducial range of a difference:

d.f. ∞ $t_{0.05} = 1{\cdot}96$ Range (±) = 1·96 × 3·16 = 6·19,

d.f. ∞ $t_{0.01} = 2{\cdot}58$ Range (±) = 2·58 × 3·16 = 8·15

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REVIEWS

INTERTIDAL ECOLOGY ON A BROAD SCALE

W. J. Dakin, Isobel Bennett & Elizabeth Pope (1948). *A study of certain aspects of the ecology of the intertidal zone of the New South Wales coast.* Australian Journal of Scientific Research, Series B, 1: 176–230, 9 photographic plates.

This study is a very welcome one, as it gives us for the first time a clear picture of the intertidal ecology of a long stretch of the Australian coast in a region outside the tropics. It is being increasingly realized at the present time, that in the past intertidal studies have been intensive examinations of small areas much more commonly than broad-scale investigations which bring out the biogeographical aspects of life between tidemarks as well as the local interrelations of limited communities. For some time the main broad-scale studies available have been those of Fischer-Piette on the English Channel, E. F. Ricketts and Torsten Gislén on the Pacific coast of North America and Stephenson and his collaborators in South Africa. Recently, lacunae in our knowledge have also been filled, for instance, by the work of R. G. Evans on the British coast, and by the series of papers entitled 'Contribution à l'étude de la répartition actuelle et passée des organismes dans la zone néritique' published by the Société de Biogéographie (Paris, 1940). Temperate Australia has hitherto been little known ecologically, though a few accounts exist, notably that of Hedley (1915) on the Sydney beaches.

The work leading to the present paper was pursued for several years and covered the whole coast of New South Wales, a stretch of about 1000 miles. While this coastline offers estuaries, sandy bays, mangrove areas and so on, it was found that the rocky ocean shore presents a clear sequence of zones which is almost the same over more than the length of the stretch studied; consequently attention was restricted to the rocky ocean coast. It is a rather straight coast running almost north and south, between latitudes 28 and 38° S., and presents a series of rocky headlands alternating with sandy beaches, many of the headlands having intertidal platforms at their feet. Annual temperature-curves for a station 4 miles off the land in the latitude of Sydney (near 34° S.) show an average surface-temperature range from about 16 to 23° C., and other data suggest a higher winter minimum (perhaps 20° C.) at the northern end of the area examined. The tidal range is in the neighbourhood of 6–7 ft. Of the common animal species between tidemarks the majority extend throughout the coast in question, which seems to represent a fairly distinct biogeographical area (Peronian province of certain systematists). There is, of course, some north to south change, and the appearance of the large Bull Kelp (*Sarcophycus potatorium*) near the southern end of the stretch is an example of this. The authors distinguish three principal zones, from below upwards, as follows:

(i) *The littoral-sublittoral fringe.* This has two subdivisions: (*a*) a kelp zone characterized by large brown algae, *Ecklonia radiata* and *Phyllospora comosa*, often replaced by the red *Pterocladia capillacea* in situations too exposed to favour the brown weeds; and (*b*) a zone typically densely populated by the large ascidian *Pyura praeputialis*.

(ii) *The mid- and upper littoral.* Here again we have two subdivisions: (*a*) the *Galeolaria* zone, characterized by a dense growth of the polychaete *Galeolaria caespitosa*, which forms masses and sheets of limy tubes resembling coral; and (*b*) a zone in which barnacles are abundant, several species being present and forming a sequence.

(iii) *The supralittoral.* The highest zone, extending well above tidal levels, has a population of littorinid snails, *Melaraphe unifasciata* and *Nodilittorina tuberculata*.

Following the account of the typical zonation is a discussion of the geographical range of the 'basic associations'. Nine ecologically important species are listed which disappear or become reduced in numbers either northward or southward on the coast; five of them being southern forms which fall off to northward, three warm-water species falling off to southward. The ninth appears to be limited to the New South Wales coast, and wanes both north and south.

The next section describes the common animals associated with the zones recognized; and throughout the paper variations in the zonation connected with differences in degree of shelter from or exposure to wave-action, and other environmental factors, are recognized. At the end is a short discussion comparing some of the features of the New South Wales coast with similar features in other parts of the world.

In his monograph on the animal geography of the sea (1935), which rather surprisingly is not mentioned in the bibliography to this paper, Ekman says that the littoral fauna of Australia is divisible zoogeographically into two regions, a tropical-subtropical and a temperate; the boundary between the two, on the east coast, lying about 35° S. in the Sydney region. He classifies the southern fauna as a warm-temperate one. From the account given by Dakin and his associates, the whole New South Wales coast has the appearance, ecologically, of a warm-temperate region, though this appearance has yet to be substantiated by a fuller analysis. Should it prove to be warm-temperate rather than subtropical, the transition from tropical to temperate must actually lie farther north than Ekman supposes, nearer 28 than 35° S. The next step will be to discover whether, as we suspect, there follows a cold-temperate region to southward of the one here described; it seems doubtful whether the *whole* of the temperate part of the Australian coast is warm-temperate.

One of the most interesting features of this stretch of Australian coast is that in some ways it presents very close ecological parallels to the South African coast, and the memoir is written in such a way as to make the results presented comparable with those of Stephenson and his associates in South Africa. The authors point out some of

the similarities, for instance the amazing low-level development in both countries of a community of leathery ascidians (*Pyura*). The comparison could actually be carried a good deal further than the authors take it, however, and they seem to have missed, for instance, the fact that their *Galeolaria* association is paralleled so exactly in South Africa by that of another polychaete, *Pomatoleios crosslandi*, that when the South African survey started the *Pomatoleios* was at first thought to be *Galeolaria*. The similarity is readily seen in some of the illustrations to the South African series, e.g. T. A. and A. Stephenson and Bright, *Ann. Natal Mus.* 9: Pl. I; T. A. Stephenson, *Ann. Natal Mus.* 10: 303 (text-fig. 8), Pls. XII and XIII. Another interesting resemblance lies in the fact that one of the characteristic low-level kelps of the New South Wales sublittoral fringe is *Ecklonia radiata*, whereas on part of the South African coast a closely similar plant, *E. biruncinata*, occupies the same ecological position, and was earlier identified with *E. radiata*.

There is an epic misquotation on p. 195. Referring to the *Pyura* community in South Africa, the authors quote Stephenson as follows: 'this leathery ascidian conceals the rock in incredible numbers, closely packed; it must cover, altogether, many inches of rock'. For 'inches', read 'miles'!

The authors have not worked out the biogeographical implications of their work in any detail, and one feels that it might have been carried considerably further in this direction. They introduce a new term 'littoral-sublittoral fringe', which is quite unnecessary, as it is the same thing as the 'sublittoral fringe' of Stephenson, a term which is beginning to come into general use. The paper, however, is an excellent contribution and represents a very decided step forward in the attempt to produce a world-wide picture of plant and animal life between tidemarks.

T. A. STEPHENSON

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by pointing out omissions and sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, Department of Zoological Field Studies, 91 Banbury Road, Oxford.

Duplicate copies of these notices can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (in two sets, May and November). Back numbers are available at half price.

Selection and abstracting has been done voluntarily by H. F. Barnes, A. Macfadyen, C. Matheson and E. Nelmes; checking by B. M. Hobby; editing by R. S. R. Fitter.

Within each section the groups are arranged in alphabetical order. Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and Brackish

Ellis, E. A. (1945). 'The rond snail, Assiminea grayana Fleming, in East Anglia.' Trans. Norfolk & Norw. Nat. Soc. 16: 82–84.

This brackish water mollusc has recently been found in some numbers on riverside ronds in east Norfolk and Suffolk, but it is not clear whether this represents an extension of range or merely that it has been overlooked. Lists of plants associated with it in three types of habitat are given, also notes on other molluscs associated with it in East Anglia.

Fowell, R. R. (1948). 'An ecological study of an enteromorpha pool.' Proc. Swansea Sci. and Field Nat. Soc. 2: 306–10.

Notes on the fauna and flora of a pool in Langland Bay, Swansea.

Pyefinch, K. A. (1947). 'The biology of ship fouling.' New Biology (Penguin Books), 3: 128–48.

A popular account of the ecology of the flora and fauna that colonize ships' hulls, and their control.

Storrow, B. (1949). 'Concerning salmon caught in the fishery district of the River Tyne.' Rep. Dove Mar. Lab. (1947), 3rd Ser. No. 10: 7–54.

Discusses the figures since 1870 with special reference to sea temperatures. The composition of the catch is fully given for 1927 to 1946.

(*b*) Fresh water

Baxter, E. W. (1949). 'Keeping lampreys alive.' Nature, Lond. 163: 911–12.

Details of tank and equipment which successfully keeps *Lampetra fluviatilis* alive by means of liberal oxygen supply, keeping the water temperature below 15° C. and not in direct light.

Éire, Department of Agriculture, Fisheries Branch (1948). 'Salmon, sea trout and eels captured during each of the six years 1947, 1946, 1945, 1943, 1941 and 1939.' Dublin, 17 pp. Price 6*d*.

Quantity and value of the catch.

Laurence, B. R. (1948). 'Waterfall fauna.' Bedfordshire Naturalist, No. 2: 56–7.

A miniature waterfall produced by the bridging of a small stream at Harlington, Bedfordshire, yielded a number of interesting Diptera, viz. *Simulium morsitans* (Simuliidae), *Dicranota* (Tipulidae), *Oxycera terminata* and *O. morrisii* (Stratiomyidae). Also several mayfly larvae (Baetidae). This type of habitat is scarce in Bedfordshire.

Lloyd, Ll. (1947). 'The biology of sewage disposal.' New Biology (Penguin Books), 2: 30–52.

A useful popular account of the ecology of sewage beds.

Stratton, L. W. (1948). 'Flood debris from the River Colne.' Trans. Herts. Nat. Hist. Soc. 23: 24–9.

Analysis of the shells of land and fresh-water Mollusca found in several bagsful of flood debris collected on the Colne at Aldenham, Herts, and a comparison with a similar analysis by A. E. Boycott of debris from the same spot in 1915.

(*c*) Land

Anon. (1948). 'Notes and observations on the effect of the severe weather on the counties' wild birds.' Leicestershire and Rutland County Rep. on Birds for 1947: 4–8.

Summarizes the effect of the severe weather from late January to early March, 1947, on the bird life of Leicestershire and Rutland under the headings of: mortality, movement, behaviour, changed feeding habits and depredations, and unusual visitors.

Ashby, C. B. (1948). 'The effects of the cold spell of early 1947 on birds in the London area.' Lond. Bird Rep. No. 12, for 1947: 39–44.

The occurrence and behaviour of birds is recorded and compared with observations made during previous cold spells.

Barnes, H. F. (1949). 'The slugs in our gardens.' New Biology (Penguin Books), 6: 29–49.

A convenient summary of data, partly derived from his papers in the *Journal of Animal Ecology*, giving determination key for species, black and white pictures, and notes on habits, numbers, biomass, seasonal breeding, etc.

Buxton, R. G. (1948). 'The effects of the weather on wild life in Norfolk during 1946–47.' Trans. Norfolk & Norw. Nat. Soc. 16: 266–71.

Covers the effect of the weather on wild life, mainly birds, from July 1946 to March 1947. July and August were very wet, and January to March very cold.

Dacker, H. (1948). 'Mortality of birds in Scotland in the cold weather of January–March, 1947.' Scot. Nat. 60: 171–6.

Day, F. H. (1947). 'Notes on Cumberland beetles. The genus *Cryptophagus* Hbst.' Northw. Nat. 22: 249–50.

Localities and habitats of 18 species recorded from Cumberland.

Fidler, J. H. (1947). 'The biology of some Yorkshire aphides.' Northw. Nat. 22: 242–8.

Notes on the bionomics of 23 species, most of which are associated with cultivated plants. Apparently no list of Yorkshire aphids exists.

Freeman, J. A. (1948). 'The insect menace to stored products.' New Biology (Penguin Books), 4: 48–73.

A popular account of the ecology and economic importance of the insect pests of stored products.

Guichard, K. M. & Yarrow, I. H. H. (1948). 'The Hymenoptera Aculeata of Hampstead Heath and the surrounding district, 1832–1947.' Lond. Nat. No. 27, for 1947: 81–111.

Contains a list of 216 species recorded in recent years and in nineteenth-century literature, with indications of their relative abundance; an account of the development of the area from forest land through heathland surrounded by open country to heathland surrounded by buildings; its present topography; a discussion of the changes that have occurred in the aculeate Hymenoptera present; lists of 48 species that have not been recorded there in the twentieth-century and 72 that occur in gardens in the area; and a map.

Hawes, R. S. (1947). 'Animal life in caves.' New Biology (Penguin Books), 3: 82–103.

A useful popular account of the biology and ecology of cavernicolous animals. It is stated that there is no good general book on the subject in English.

Key, H. A. S. (1948). 'The hard winter and its effect on bird life.' Bedfordshire Naturalist, No. 2: 37–41.

Describes the effect on birds in Bedfordshire of the severe weather between December 1946 and March 1947.

Macfadyen, A. (1949). 'Micro-climates.' Science News, 12: 128–44.

A useful popular account of the importance of micro-climates in ecological work, with some description of current methods of recording micro-climates.

Niblett, M. (1948). 'Plant gall records for 1947.' Lond. Nat. No. 27, for 1947: 78–80.

Includes records for Cynipidae, Cecidomyiidae, Trypetidae, Coleoptera, Psyllidae, Aphididae and Eriophyidae.

Rooke, K. B. (1948). 'The effects of the cold spell (January to March 1947).' South-Eastern Bird Report for 1947, 71–83.

Notes based largely on personal observation in east Dorset and south-west Hampshire, with some reference to the status of birds in south Devon in April, under the headings of: birds found dead; causes of death; unusual movements; list of species affected.

Swaby, R. J. (1949). 'The relationship between micro-organisms and soil aggregation.' J. Gen. Microbiol. 3: 236–54.

In experiments cultures of micro-organisms, especially fungi, improve crumb structure of soil, but many factors, including microbial antagonisms, reduce this effect in nature and, although the action of microbes may partly explain improved crumb structure after addition of organic materials to the soil, permanent crumb structure of many soils must be mainly due to other causes.

Turk, F. A. (1947). 'Myriapodological Notes, II.' Northw. Nat. 22: 226–34.

Includes comments on the occurrence of *Lithobius forficatus* at high altitudes, in which it is stated that this myriapod, which rarely occurs above 800 ft. in southern Britain and is replaced at these altitudes by *L. variegatus*, was the dominant species under boulders at over 1000 ft. in Scotland; *L. variegatus* was not present. There are also eight additional records of Diplopoda from caves in Somerset and South Wales.

Wilson, G. F. (1948). 'Two injurious aphid pests of conifers.' J. Roy. Hort. Soc. 73: 73–80.

Gives distribution, recorded host plants at Wisley, Surrey, symptoms of attack, description, biology and control measures for *Neomyzaphis* (*Myzaphis*) *abietina*, which occurs on various conifers, and *Neochmosis* (*Panimerus*) *cupressi*, which is known only on *Cupressus macrocarpa*.

Wilson, G. F. (1948). 'The bulb and stem eelworm in relation to garden plants.' J. Roy. Hort. Soc. 73: 335–45.

Gives the distribution, principal host plants, description, life history, symptoms of attack, biological races, means of dispersal and methods of control of *Anguillulina dipsaci*.

(*d*) Small islands

Williamson, M. H. (1949). 'The habitat distribution of lycosids (Araneae) on Skokholm.' Rep. Skokholm Bird Observatory for 1948: 20–24.

An examination of Gause's contention that species with a similar ecology cannot exist together in the same habitat in the light of the seven species of lycosid spiders known to exist on the Pembrokeshire island of Skokholm. It was established that in two areas two related species occurred together, and considered that the hunting differences between the two species were sufficient to prevent them from competing.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Edwards, V. C. Wynne- (1948). 'The nature of subspecies.' Scot. Nat. 60: 195–208.

A review of the taxonomic tool of trinomialism in the light of modern population studies and genetical knowledge. The idea that populations rather than individuals are the basic units of evolution is emphasized. It is concluded that differences between subspecies are equally adaptive to those between species and genera, and that systematists should take care not to abuse their tool by designating subspecies too finely distinguishable from each other.

Fitter, R. S. R. (1948). 'Contributions to the bibliography of the natural history of the London area. I. Mammals, reptiles and amphibia.' Lond. Nat. No. 27, for 1947: 76–78.

A list of 51 papers and monographs.

Morison, G. D. (1948). 'Thysanoptera of the London Area. Part II. Key to British genera and species of Thysanoptera.' Lond. Nat. 27, suppl.: 37–75.

This concluding part contains notes on the distribution in Britain and London and on the food-plants of the species, with the months in which they are recorded on plants, as well as the genera and species keys.

3. PARASITES

Brown, E. S. (1949). 'Vorticellids (Protozoa: Ciliophora) epibiotic on larvae of the genus *Aëdes* (Dipt., Culicidae).' Ent. Mon. Mag. 85: 31–4.

An instance of marked intra-generic selection of host, *A. rusticus* larvae seldom being infested.

Dallimore, W. (1949). 'A serious scale insect on yew.' Quart. J. For. 43: 79.

Pulvinaria vitis var. *ribesiae* has occurred on yew, a host not previously recorded for Britain, at the National Pinetum at Bedgebury, Tunbridge Wells, and at Dorking, Surrey, and has been sent to Kew Gardens from various parts of the country.

Day, C. D. (1947). 'British tachinid flies (Tachinidae-Larvaevoridae and Calliphoridae).' Northw. Nat. 22, suppl.: 97–150.

This concluding part completes species table 19 and gives two more. Systematic lists of the hosts attacked and the flowers visited by tachinids in Britain, a list of synonyms for the genera and species and one of synonymous descriptive terms, and wing-check tables for 232 species, with figures of the wings of 148, are also given.

Dunn, J. A. (1949). 'The parasites and predators of potato aphids.' Bull. Ent. Res. 40: 97–122.

The parasites and predators found attacking *Myzus persicae*, *Macrosiphum solanifolii* and *Aulacorthum solani* are dealt with individually and in many cases figured. *Aphidius avenae* was the chief primary parasite while *Asaphes vulgaris* and *Lygocerus testaceimanus* were the most numerous hyperparasites. The effect and importance of both types of parasite on the aphid populations are discussed.

Predacious syrphids included *Platychirus manicatus* and *P. immarginatus* whose life histories were previously unknown. *P. manicatus* was invariably accompanied by *P. scutatus*. Less frequent in occurrence but more effective was *Syrphus balteatus*. *Coccinella septempunctata* presents a total check when it occurs in swarms during early August, but parasites and predators appearing about mid-July seldom interrupt the growth of the aphid populations until the infestation is stable or declining.

Potatoes grown in a small garden plot give a more detailed indication of the type of natural balance achieved by the indigenous species of insects. Fungus and rain here became important factors. But again the results emphasize that the combined native enemies interfere with their aphid hosts at too late a stage to prevent colonization.

Ellis, E. A. (1948). 'A snail and bird parasite.' Trans. Norfolk & Norw. Nat. Soc. 16: 329–30.

In July and August 1947 several amber snails (*Succinea putris*) at Wheatfen Broad, Yare valley, Norfolk, were found to be infested with a bird fluke-worm, *Distomum macrostomum*.

Kendall, S. B. (1949). '*Lymnaea stagnalis* as an intermediate host of *Fasciola hepatica*.' Nature, Lond. 163: 880–1.

Experiments showed that the liver fluke can complete its development cycle in this species of fresh-water snail, though so far only in young specimens. As *L. stagnalis* does not live in marshes, the practical significance may not be great.

Lapage, G. (1947). 'The menace of the roundworm.' New Biology (Penguin Books), 3: 49–81.

A popular account of the biology and economic importance of nematode worms, with special reference to those infesting sheep.

4. FOOD AND FOOD HABITS

Campbell, J. W. (1948). 'Black-headed gulls feeding on caterpillars.' Scot. Nat. 60: 54–5.

During a plague of caterpillars, mainly *Cheimatobia brumata* and *Hybernia defoliaria*, on oaks in the upper Tay valley, Perthshire, in May and June 1947, many species of birds came to feed on them in large numbers. In particular, hundreds of *Larus ridibundus* were frequently seen picking the larvae from the ground under the trees, both on roads through the woods and in the interior of woods.

Ellis, E. A. (1948). 'Coypus eating marsh plants.' Trans. Norfolk & Norw. Nat. Soc. 16: 328–9.

Brief observations on the plants eaten by feral *Myocastor coypus* at Wheatfen Broad in the Yare valley, Norfolk, in 1947.

Ellison, N. F. (1947). 'Wading birds and cockles.' Northw. Nat. 22: 270.

Three records of dunlin (*Calidris alpina*) killed by cockles gripping their bills or, in one case, feet. A fourth, living dunlin was seen trying unsuccessfully to dislodge a cockle from its bill.

Höhn, E. O. (1948). 'The food and feeding movements of London mallards.' Lond. Bird Rep. No. 12, for 1947: 36–8.

The gullet and stomach contents of 48 mallards (*Anas platyrhyncha*) shot in St James's and Regent's Parks, are summarized; vegetable matter, mostly unidentifiable, predominated over animal remains. Local feeding movements from the Parks occur, and at St James's Park, most birds leave for unknown feeding areas each evening during September–November; the gizzards of several were crammed with wheat grains. Numbers increase during winter, and the birds appear to disperse fairly widely, as several ringed in the summer of 1944 were not subsequently seen.

Jørgensen, C. B. (1949). 'Feeding-rates of sponges, lamellibranchs and ascidians.' Nature, Lond. 163: 912.

Feeding rates were measured by the rate of disappearance of colloidal graphite particles introduced into the water, the density of the latter being determined photometrically. The rates are expressed per mg. of amino-nitrogen of the animals, instead of per unit weight or length. The sponges *Grantia compressa*, *Sycon coronatum*, *Halichondria*, the lamellibranch *Mytilus edulis*, and the ascidians *Molgula* sp., *Ciona intestinalis*, all took up particles at a rate having much the same order of magnitude, but ranging from higher values in *Molgula* and *Sycon*, to less than half these rates in *Mytilus* and *Halichondria*. In the sponges and ascidians the rate was independent of the particle size of the 'food'.

5. POPULATION STUDIES

Anscombe, F. J. (1948). 'On estimating the population of aphids in a potato field.' Ann. Appl. Biol. 35: 567–71.

An unbiased method is described in which a definite proportion of a number of plants is sampled and also a more rapid method of stratified sampling.

Barnett, A. (1947). 'The war against rodents.' New Biology (Penguin Books), 2: 9–29.

Popular account of the ecological relationship between man and certain rodents, mainly rats, with some details of the wartime control campaign against them in Great Britain and the research which underlay it.

Baxter, E. V. (1948). 'A century's changes in Scottish ornithology.' Scot. Nat. 60: 11–19.

Summarizes the changes of status of birds in Scotland over the past hundred years.

Brambell, F. W. R. (1948). 'Prenatal mortality in mammals.' Biol. Rev. 23: 370–407.

Mainly methods of estimating prenatal mortality. Stresses the need for counts of implantation sites to supplement those of corpora lutea and of surviving embryos. Data obtained indicate a 10–13% loss of ova before implantation in wild rabbits and that not less than 35% of litters surviving implantation are lost *in toto*. At least 43·3% of ova do not survive parturition.

Brambell, F. W. R. (1948). 'Studies on sterility and prenatal mortality in wild rabbits. Part IV. The loss of embryos after implantation.' J. Exp. Biol. 25: 241–69.

It is shown statistically that part of the loss of embryos is falling on litters as units, i.e. not wholly at random on embryos as units. The greater the number of embryos in a litter which have become implanted the less the probability of the litter being lost. Most litters are lost between the 11th and 15th day of gestation. Loss of litters is inversely proportional to body weight of mothers and is greater in lactating animals. There are geographical and seasonal variations in the incidence of loss and the rate is especially high at the beginning of the breeding season.

Broadbent, L. (1948). 'Methods of recording aphid populations for use in research on potato virus diseases.' Ann. Appl. Biol. 35: 551–66.

Methods of counting aphids infesting potato crops are reviewed and discussed. It is concluded that an estimate of the number of aphids per plant is better for virus research than the number per 100 leaves. A method of estimating the number of aphids per plant is described as well as a method based on the percentage of leaves infested.

Campbell, B. (1947). 'Field notes on the breeding of the roseate tern (*Sterna d. dougallii* Mont.) in Scotland.' Northw. Nat. 22: 174–7.

Notes are given on the development of the first large colony of roseate terns to be established on the east coast of Scotland. Numbers on a very small island, of which less than one-sixth was above high-water mark, increased from 3 or 4 pairs in 1933 to an estimated total of 60–75 pairs in 1945. The percentage of nests that contained two eggs or young birds was 37·2, which corresponds with that found in a large Irish colony. Most birds nested in deep sites, apparently from preference and in contrast with site preferences noted at other colonies. Some data on the numbers of other birds that breed on the island are included.

Currie, P. W. E. (1948). 'Black redstarts in the London area.' Lond. Bird. Rep. No. 12, for 1947: 32–4.

Six pairs of *Phoenicurus ochrurus* are known to have bred in the City of London in 1947, and two others may have done so. Data on breeding pairs collected throughout the season are summarized. Mortality among young birds disturbed through ringing was high. One male apparently spent the winter in the area, and there are some eleven non-breeding records from Inner and three from Outer London.

Evans, A. C. & Guild, W. J. McL. (1948). 'Studies on the relationships between earthworms and soil fertility. IV. On the life cycles of some British Lumbricidae.' Ann. Appl. Biol. 35: 471–84.

The cultures of worms for cocoon production were kept in screw-topped glass jars two-thirds filled with moist soil and a layer of moist bullock droppings. The number of worms per jar and size of jar varied with the size of the worms, in the case of the largest species, *Lumbricus terrestris*, 3 individuals were kept in 5-pint jars. The worms were transferred to fresh soil and bullock droppings every fortnight and the cocoons were recovered by washing the soil through sieves with water. The cocoons were kept in beakers containing clean sand and water. On emergence the worms were transferred singly to glass tubes, 3 × 1 in., capped by a short piece of rubber tubing of $\frac{7}{8}$ in. diam. into which a piece of brass gauze was sealed with rubber solution. The smaller species were reared to maturity in these tubes but the larger species were later transferred to jars varying in size from $\frac{1}{2}$ lb. honey jars to 5-pint jars.

The rate of cocoon production of 14 species differs from species to species and is greatly affected by soil temperature, moisture and food supply of the adult worms. Only two species frequently produced more than 1 worm per cocoon, twins were recorded on one occasion. The incubation period of the cocoons and growth period to sexual maturity varies from species to species and also depends on the time of year at which the cocoons are deposited and the young worms emerge.

Evans, A. C. & Guild, W. J. McL. (1948). 'Studies on the relationships between earthworms and soil fertility. V. Field populations.' Ann. Appl. Biol. 35: 485–93.

The ploughing of a permanent pasture in spring was not followed by a reduction of the population during the first 6 months, but further arable cultivation did greatly reduce the number of earthworms. Some trends in population changes during nearly 1 year are described for five common species. The population of a permanent pasture did not show appreciable change for a period of nearly 3 years but that of a ley, in its first year following arable, showed a significant increase. Leys, 4–7 years old, carry a total population similar to that of permanent pastures, but with differing proportions of certain species.

Fidler, J. H. (1949). 'A three years' survey of potato aphids in north-east Yorkshire.' Ann. Appl. Biol. 36: 63–75.

Counts of aphids were made during three consecutive seasons on selected fields on the higher land in north-east Yorkshire. They are related to the geographical, climatic and biological factors of each field.

Finnis, R. G. (1948). 'A survey of the rookeries of the Isle of Thanet: spring, 1947.' Bird Rep. for 1947: 66–69.

In an area of about 40 sq.m. of agricultural land and suburban gardens, 1255 nests were found in 17 rookeries, representing an increase of 230 nests over 1944 despite the severe weather of early 1947, and a density of 30·6 nests per sq.m. In recent years several small rookeries have been abandoned in the towns of the coastal strip.

Kesteven, G. L. (1948). 'Vital statistics of fish populations.' New Biology (Penguin Books), 4: 99–118.

A popular account of recent fish population research.

May, E. S. (1949). 'Recent changes in status of some local birds.' Trans. Hertfordshire Nat. Hist. Soc. 23: 45–53.

In Hertfordshire over the past 24 years the following species have increased: great crested grebe, gulls, redshank, dunlin, green sandpiper, little ringed plover, tufted duck, pochard, shoveler, carrion-crow, magpie, green woodpecker and goldfinch. The corncrake and greenfinch have decreased over the same period. The black-necked grebe, which was attempting to establish itself as a breeding species at the beginning of the period has failed to do so. Reasons for these changes are suggested.

Miles, M. (1945). 'Wireworms and war-time agriculture.' New Biology (Penguin Books), 1: 86–95.

Popular account of the life history of wireworms (mainly *Agriotes* spp.) and the problems of controlling them during the war-time ploughing-up campaign; also refers to a survey of wireworm population carried out during the war.

Parrinder, E. R. (1948). 'The census of great crested grebes, 1947.' Lond. Bird Rep. No. 12, for 1947: 35–6.

There were 228 adults of *Podiceps cristatus* in the London area in the breeding season of 1947, showing a decrease of 18% over the total for 1946, when, however, six more waters were visited. The decrease is attributed partly to the partial or complete filling in of waters and to human interference, but chiefly to the severe winter of 1946–7. Grebes were found on six waters that were not visited in 1946, and the number of breeding pairs had increased to 63.

Richards, O. W. (1947). 'Observations on grain-weevils, *Calandra* (Col., Curculionidae). I. General biology and oviposition.' Proc. Zool. Soc. Lond. 117: 1–43.

A detailed study of the development and breeding of *Calandra granaria* and of two strains of *C. oryzae*, with special reference to the influence of environmental factors. Includes data and discussion of the decrease of oviposition rate at increasing densities of population, reported in some experiments.

Salt, G. & Hollick, F. S. J. (1949). 'Studies of wireworm population. III. Some effects of cultivation.' Ann. Appl. Biol. 36: 169–86.

The decline in numbers was accompanied by a change in the composition of the wireworm population; the marked inverse correlation between the number and size of larvae under grass progressively altered towards uniform numbers of the different size groups. Three groups of factors are suggested as being responsible for the progressive decline in numbers in the years following the ploughing-up of grassland; namely (1) immediate effects of cultivation, i.e. mechanical injury and exposure to bird and other predators, (2) the physical conditions of cultivated soil might be responsible directly through its different texture or composition or indirectly through change in the flora and fauna, and (3) the failure of replenishment by decreased oviposition. The evidence regarding (2) was insufficient to prove the point.

Singh, B. N. (1949). 'The effect of artificial fertilizers and dung on the numbers of amoebae in Rothamsted soils.' J. Gen. Microbiol. 3: 204–10.

Both types of treatment result in increased populations of amoebae, both active and active + cystic. The latter category are also more numerous in dunged than in artificially fertilized soil.

6. MIGRATION, DISPERSAL AND INTRODUCTIONS

Bainbridge, R. (1949). 'Movement of zooplankton in diatom gradients.' Nature, Lond. 163: 910–11.

In an attempt to test by direct experiment the 'plankton exclusion' and 'plankton grazing' hypotheses, three species of estuarine Crustacea (*Neomysis vulgaris*, *Eurytemora hirundoides* and *Macropsis slabberi*) were released in gradients of diatom density. No avoidance of the diatom concentrations was noted. But it is stated that these Crustacea are estuarine forms for which no exclusion behaviour has been observed or claimed in the field.

Brian, M. V. & Brian, A. D. (1948). 'Observations on rook movements and winter roosts in part of Hertfordshire.' Trans. Hertfordshire Nat. Hist. Soc. 23: 30–6.

Three roosts were located and the areas from which they drew their populations roughly determined.

Broadbent, L. (1949). 'Factors affecting the activity of alatae of the aphids *Myzus persicae* (Sulzer) and *Brevicoryne brassicae* (L.).' Ann. Appl. Biol. 36: 40–62.

An apparatus consisting essentially of a wooden cabinet with a ground-glass top with a movable window for testing the frequency of flights of aphids under different conditions of temperature, relative humidity, light and pressure is described. Results are given and it is concluded that changes in microclimates in crops are adequate to influence the flight of aphids and consequently the spread of virus diseases.

Dannreuther, T. (1948). 'Insect immigration: Scotland an end point.' Scot. Nat. 60: 74–81.

Observations from Scotland of migrant butterflies and moths are of particular importance, since except in the rare cases where a few reach Iceland and even the Arctic, the Scottish mainland and islands represent the normal land terminus of such migratory movements.

Edmondson, T. (1947). 'Inland passage of the white wagtail.' Northw. Nat. 22: 269.

Observations in 1942–7 show that *Motacilla alba* migrates regularly in spring to the inland waters of Leigh and Wigan flashes, S. Lancashire. Its passage along the S. Lancashire coast has been recognized for some time.

Edmondson, T. (1947). 'Unusual inland passage of terns.' Northw. Nat. 22: 269–70.

Large numbers of common and arctic terns (*Sterna hirundo* and *S. macrura*) were seen at Leigh Flash, South Lancashire, in spring 1947, and a summary of the combined numbers observed and the wind data for each day between 20 April and 10 May is given. *S. macrura* was more abundant than would formerly have been expected. The movement was correlated with strong southerly to westerly winds, and ceased with the onset of easterly winds.

Munro, J. H. B. (1948). 'The rook roosts of the Lothians, winter 1946–47.' Scot. Nat. 60: 20–9.

An account of a survey by the Midlothian Ornithological Club in the counties of East, Mid- and West Lothian, Scotland.

Newell, G. E. (1949). 'Occurrence of a species of *Clymenella* Verrill (Polychaeta, fam. Maldanidae) on the North Kent coast.' Nature, Lond. 163: 648.

A species apparently of the *torquata* group thought to be confined to the coasts of North America, is moderately common in the intertidal zone at Whitstable, near ordinary L.W.M. It may prove to be a recent immigrant like *Urosalpinx* and *Crepidula*.

[**Palmer, R.**] **(1948).** 'The Colorado beetle in Bedfordshire.' Bedfordshire Nat. No. 2: 57–58.

Summarizes six occurrences of this immigrant beetle pest in the county during July and August 1947.

Smith, T. Leslie (1948). 'Growth and decline of an artificial grouse moor.' Scot. Nat. 60: 99–106.

Repeated introductions of *Lagopus scoticus* were made on the exposed coastal moorland of Tentsmuir, Fife, from 1876 to 1921, and a stock was established, which had its ups and downs and was augmented from time to time by natural immigrants, probably from the moors of Angus. In 1924 the greater part of the moor was bought for afforestation, and thereafter the stock remained steady, but bags declined from 83 brace in 1935 to one brace only in 1943 and none thereafter.

Vevers, G. M. (1948). 'The fat dormouse and other wild mammals at Whipsnade.' Bedfordshire Nat. No. 2: 42–4.

Since 1931, 33 specimens of *Glis glis* have been caught in the lofts of a wooden bungalow at Whipsnade, Bedfordshire, about 7 miles from the original point of introduction at Tring, Hertfordshire.

Walker, F. T. (1949). '*Tellina magna* found in Orkney.' Nature, Lond. 163: 682.

One empty bivalved example of a species native to eastern America was found among seaweed cast up near Stromness. It has not previously been recorded on this side of the Atlantic.

7. REPORTS OF ORGANIZATIONS

Elder, H. F. D. (1948). 'Isle of May Bird Observatory: Report, spring and autumn 1946.' Scot. Nat. 60: 177–80.

The observatory on this island at the mouth of the Firth of Forth reopened on 13 April 1946, after a closure lasting since 21 September, 1938. Ringing and observation on migration was carried out irregularly in the spring up to 10 June, and almost continuously from 15 August to 11 October.

Elder, H. F. D. (1948). 'Isle of May Bird Observatory and Field Station: Bird Report, spring and autumn 1947.' Scot. Nat., 60: 181–7.

The change in title indicates the expansion of the interests of the observatory to cover all natural history, under the aegis of a committee largely appointed by the Scottish universities. Ornithological observations were made on most days from 5 April to 8 June, and from 9 July to 28 October.

London Natural History Society (1948). 'The Epping Forest Survey. Sixth Year. Report on the Survey of the Ludgate Plain area, 1946–7.' Lond. Nat. No. 27, for 1947: 66–74.

This report contains a general descriptive account of the topography of the area, including notes on the soil and vegetation and a map; the results of 20–30 counts of birds (of which 54 species were observed) and a comparison of their frequencies with those observed for the same species in other areas; a list of other vertebrates (mammals, grass snake, frog); and another of plant galls due to Cynipidae and Cecidomyiidae.

London Natural History Society (1948). 'The survey of Bookham Common. Sixth year.' Lond. Nat. No. 27, for 1947: 49–65.

A review of the work during the year by C. P. Castell (pp. 49–51) includes a summary of ornithological observations based on a report by P. W. E. Currie. Other papers comprise a list of the fresh-water molluscs found in ponds, streams and ditches between March 1946 and November 1947, with notes on the species and their distribution and a table and graph showing seasonal fluctuations of five species in one pond, by C. J. F. Bensley (pp. 51–55); habitat notes on the 28 land molluscs (of which over a third are slugs) recorded in woodland, marsh and open grass in March–July 1947, by A. E. Ellis (pp. 56–59); a short account of the abundance, distribution and habitats of five wood-lice (Oniscoida) recorded from the Common, with a brief discussion of their humidity requirements (pp. 59–60) and a note of the occurrence of two Amphipods (p. 60), also by A. E. Ellis; and a list, with dates, localities and indications of abundance, of beetles of the sub-orders Sternoxia, Heteromera and Longicornia, of which about a quarter of the total for the British Isles occur on the Common, and Teredilia, of which barely one-sixth are present, with additions to previous lists of Rhyncophora, Phytophaga, and Malacodermata, by A. M. Easton (pp. 61–5).

Lundy Field Society (1949). Second Annual Report, 1948. 50 pp.

Includes an annotated list of the birds recorded on this island in the Bristol Channel during the year, with special notes on the Manx shearwater (*Puffinus puffinus*) and the fulmar petrel (*Fulmarus glacialis*), a brief account of the marine ecology, additions to the list of land flora, and miscellaneous notes on the terrestrial invertebrates.

Oundle School Natural History Society (1948). Annual Report for 1947. 32 pp.

Contains phenological observations for 1946–7, and lists of birds, butterflies and moths, including Micro-lepidoptera, for 1947.

Skokholm Bird Observatory (1949). Annual Report for 1948. 36 pp.

Includes lists of the mammals, birds, reptiles, Amphibia and Lepidoptera of this Pembrokeshire island, together with accounts of the ecological work and colour ringing of birds done by students at the observatory during the year. There are brief accounts of work on the life history of the wheatear (*Oenanthe oenanthe*) and the oystercatcher (*Haemantopus ostralegus*).

Yorkshire Fishery District (1949). Eighty-second Annual Report on the salmon, trout, and freshwater fisheries in Yorkshire (1948) (by R. W. Ward). 36 pp.

An account of finances, prosecutions, working of the hatchery, rainfall pollution; and numbers of salmon and sea trout taken since 1888. Almost the entire fish population of a lake was lost in July 1948, through a combination of high oxygen content and strongly alkaline waters.